

The American Midland Naturalist

Devoted to Natural History, Primarily that of the Prairie States

Founded by J. A. Nieuwland, C. S. C.

Edited by Theodor Just

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Brother Marie - Victorin, F.S.C.

1885-1944



Françoise M. Danserau del.

Brother Marie-Victorin, F.S.C.

Brother Marie-Victorin

1885 - 1944

Pierre Dansereau

It is difficult, at this time, to outline the significance of Brother Marie-Victorin's work. We, who were closely associated with him, are for the present too deeply grieved to appreciate it in the cold light of history. We cannot yet separate the man and the scientist.

And after all, it may be that there is no need to do so. It may be that the greatest thing he has taught us is to be human as he was. In the course of a period when it was fashionable for so many scientists to be cold and skeptical, he neither chose to imitate that mock objectivity, nor hesitated to lend the full color of his strong personality to his writings. This implies no departure from orthodox methods of scientific practice, because those who are familiar with his taxonomic and geobotanical papers remember well the firm design and faultless dialectics which served to present his materials.

He was a great man of science, and he was a great man. To those who came in contact with him, the latter was the more evident; he made numerous friends and gained many admirers in the course of an exceptionally varied and fecund career. Many of them were neither botanists, nor even scientists, but all appreciated that whatever he turned to, he was capable of assimilating and changing as only a creative personality can. In many young French Canadians he engendered that rare and essential enthusiasm which is the point of departure for original endeavor. To many, the very existence of such a man was a comfort and held valuable promises. Contact with a mind in which faith, intelligence and an intimate knowledge of scientific facts as well as artistic and poetic revelations coexisted so harmoniously, was stimulating. That one mind should firmly grasp such diversity and make it its own, and show no trace of pedantic encyclopedism, was no less admirable. For science had come to most of them under a dry-packed foreign label or had been shamelessly distorted by teleological presentation. Art and literature, on the other hand, were mostly bookish or vague, and usually without any relation to everyday life, and much less so to the natural environment in which they lived.

Brother Marie-Victorin was born Conrad Kirouac, in 1885 at Kingsey Falls, Quebec. His family, as the name implies, was of Breton descent, and it can well be argued that the blood of Jacques Cartier, the discoverer of Canada,

of Châteaubriand, the great Romantic, and that of so many pioneers and poets produced by that rugged peninsula, still ran very pure in his veins. The well known perseverance and stubbornness of the race were also his.

As a boy, he lived in the city of Quebec, where his father was a well-to-do merchant. He attended the *Académie Commerciale*, an institution which was then, and still is, under the direction of the Brothers of the Christian Schools. At the tender age of 15, he entered that congregation and was sent to Montreal for his novitiate. Strangely enough, the Brothers' house stood on the very spot where the Montreal Botanical Garden was later to be founded by Brother Marie-Victorin.

For many years until 1920, when he was called to the *Université de Montréal*, he taught at one of the Brothers' schools, especially at *Longueuil*, on the south shore of the St-Lawrence, opposite Montreal. His creative abilities were early recognized by his superiors and he was encouraged to publish. This he did at first in a literary vein. His gift for description and his intense patriotism found adequate expression in a series of folk tales produced in newspapers and periodicals, which was eventually reprinted in book form. In 1919 the "*Récits laurentiens*"¹ and in 1920 the "*Croquis laurentiens*"² were issued and met with considerable success. The freshness of style, the directness of the simple stories and the vividness of the descriptions struck a new note in French Canadian literature. The obvious influence of the XIX century French romanticists could not obscure the writer's genuine gifts. Regardless of how much their form may be reminiscent of that school, the feeling behind it was genuine and the images evoked by the author were inspired by typical traits of Canadian life. In other words, the critics welcomed Marie-Victorin's tales as a breath of fresh air, because he was almost the first native writer who described Canadian nature with an accuracy backed by an unflinching poetic touch.

Meanwhile, Brother Marie-Victorin taught geometry, physics and the natural sciences at the *Collège de Longueuil*. It was a heavy schedule and involved rather heterogeneous material. He also found time to direct a group of boys in extra-curricular studies.

It is hard to imagine how he could indulge in botanical research as well.

¹ MARIE-VICTORIN, F. 1919—*Récits laurentiens*. 207 pp. Frères des Ecoles Chrétiennes, Montréal.

² MARIE-VICTORIN, F. 1920—*Croquis laurentiens*. 304 pp. Frères des Ecoles Chrétiennes, Montréal.

His earliest publication is dated 1908.³ He was the first in America to signal the invasion of the flowering rush (*Butomus umbellatus*). In the years between 1908 and 1915, he published a few botanical notes every year, mostly in the *Naturaliste Canadien*, a scientific periodical issued by Laval University in Quebec.

In 1916, appeared his first important work, the flora of Temiscouata County⁴, in the Lower St-Lawrence. Meanwhile, he had managed to gather the essentials of a botanical library, had established correspondence and exchanges with other botanists,⁵ Canadian and foreign.

In 1920, the Faculty of Sciences of the *Université de Montréal* was founded, and he was called upon to inaugurate the teaching of Botany. Two years later, he was appointed Professor of Botany. He himself told the story of the Botanical Institute,⁵ its more than humble beginnings, its struggles and achievements. In it he stressed the part played by his assistants and collaborators in the development of that institution, and made it plain that no one man could have accomplished so much in so little time, could have amassed such collections, established so many useful contacts and organized such a workable and orderly unit. But it is equally obvious that only an outstanding and exceptionally vigorous personality could have conceived, created and upheld the structure of such an edifice. However, Brother Rolland-Germain should be mentioned here. A Frenchman by birth, a Canadian by adoption, Brother Rolland has been Victorin's collaborator from the very beginning, as the citations of exsiccata from almost any North American monograph of a species extending into Quebec will testify. The keenness of his mind, the acuteness of his observation, and his fine sense of humor have stood Victorin in good stead throughout his brilliant career.

Victorin was a man who dared. He came at a time when the sciences were not in good repute in the French Canadian system of education, particularly so I should say, as far as the natural or so-called *minor* sciences ("les petites sciences") are concerned. He was not deterred in obtaining wide recognition for botany by the protests of many educators, who claimed that it was developing beyond its proper proportions. It was only too clear to him that botany

³ MARIE-VICTORIN, F. 1908—Additions à la flore d'Amérique.—*Naturaliste Canadien* 35(5):65-67.

⁴ MARIE-VICTORIN, F. 1916—La flore du Témiscouata; mémoire sur une nouvelle exploration botanique de ce comté de la province de Québec. 125 pp. Laflamme, Québec.

⁵ MARIE-VICTORIN, F. 1941—Histoire de l'Institut Botanique de l'Université de Montréal, 1920-1940.—*Contrib. Inst. Bot. Univ. Montréal*, 40.

was not overdeveloped but that some of the other sciences — and arts, for that matter! — were underdeveloped!

It is hardly possible, here and now, to draw even in a few brief strokes the background of Montreal in the early twenties and to outline the difficulties of those courageous men who created the Faculty of Sciences at the *Université de Montréal*.⁶ Most of them, till then, had had no opportunity to travel or to study abroad. They had to make the best of local resources and of correspondence. For his part, Brother Marie-Victorin has repeatedly acknowledged his indebtedness to Professor M. L. Fernald. Indeed, anyone at all familiar with his work can detect the unmistakable stamp of the great Harvard botanist, whose influence in America is so deservedly far-reaching. The procedure in Victorin's taxonomic monographs, his very concept of species and many of his geobotanical theories are in full accord with Fernald's. However, his early interest in genetics, his experience with African and European floras and, above all, his very keen personal sense of observation and peculiar feeling for analogies enabled him to develop an original point of view on botanical problems. A paper of his published by this journal in 1938⁷ brings out the acuity of his vision, his wide and varied experience and remarkable power of synthesis.

Again, it is difficult to estimate the value of Victorin's writings. His contributions to taxonomy, floristics and geobotany are assuredly important to North American botany at a time when the inventory of our flora has not yet been completed and when we are just beginning to analyze the dynamic aspects of species, of floras and of vegetation at large. In his "Flore Laurentienne,"⁸ these diverse points of view converge, although the floristic aspect is the most obvious. This flora was conceived and written in an entirely new form. It was the first flora to include chromosome numbers. The marginal notes appended to almost every species contain a wealth of information, much of it first hand and unpublished elsewhere, which is useful to the geneticist, the ecologist, the agronomist, the silviculturist or the student of folklore as well as to the teacher.

Less known outside of Canada, however, is Brother Marie-Victorin's

⁶ DANSEREAU, PIERRE. 1944—Science in French Canada.—*Scient. Monthly* 59(348):188-194; (349):261-272.

⁷ MARIE-VICTORIN, F. 1938—Phytogeographical problems of Eastern Canada.—*Amer. Midl. Nat.*, 19:489-558.

⁸ MARIE-VICTORIN, F. 1935—*Flore laurentienne*. 927 pp. Frères des Ecoles Chrétiennes. Montreal.

influence on education and research. I have attempted to describe elsewhere⁶ the pattern of education in French Canada and to outline the recent growth of science from a liberal arts background. I shall not redraw the picture here but wish to stress the leading rôle of Victorin in the coming of age of French Canadian universities. The natural sciences there did not begin with him any more than taxonomy did with Linnaeus or physiology with Claude Bernard. But he was our first native scientist to speak the international language of science, to give back to the world something of what the world had been giving us for such a long time. He acquired a fine reputation as an authority in a community in which authority is recognized, and he made full use of his prestige to further the interests of science.

This influence can be traced in many realms of activity: no one is likely to forget the leading rôle he played in the foundation of institutions such as the Botanical, the Biological and the Geological Institutes at the *Université de Montréal*, the Junior Naturalists' Clubs, the Montreal Botanical Garden, and the *Association Canadienne Française pour l'Avancement des Sciences*. Many of his courageous public addresses have had far-reaching effects, such as his plea for the development of geology,⁹ which was soon followed by the creation of Laval University's *École des Mines*.

Research in taxonomy and floristics can be carried on with relatively humble means. By comparison it has repeatedly been pointed out that physiology, chemistry and the experimental sciences generally could not start with such limited facilities. No doubt that is true enough. But their recent development and practice in French Canadian institutions was none the less considerably aided by the progress of botany, even if not in a material sense, then at least through the increased prestige of science. The standards set by Victorin, his accomplishments and his success are therefore to a greater or lesser extent connected with the origin of later developments of these sciences in French Canadian universities.

Those who have known him will best remember Brother Marie-Victorin from one of the numerous excursions he used to take with his assistants, colleagues or friends. The last 25 years of his life were spent searching the countryside for yet undiscovered species or curious and unrecorded forms. He had developed an extraordinary knack of spotting the unusual and recognizing the familiar from a moving automobile.

⁹ MARIE-VICTORIN, F. 1937—Pour un Institut de Géologie. 16 pp. Société Canadienne d' Histoire Naturelle, Montréal.

To those of us, who have had the privilege of accompanying him on these trips, each was rich in discoveries and eventful in many other ways. We were sure to return not only with a sheaf of newly acquired facts but with the sense of having been touched by the light and the warmth of a rich and powerful personality.

We would stop by the roadside and pick up some tiny *Euphrasia* or some coarse *Solidago*. In a few words he would make it live, he would project its form into time and space, all the while fingering its leaves, its flowers or fruits with hands that felt its very substance. He did to it with a few simple words what Leonardo da Vinci did to the violets and stars-of-Bethlehem he drew: he made them seem more real than the living plant.

It was on such an excursion that he died — as no doubt he would have chosen to. He died on the roadside not very far from his birthplace.

—PIERRE DANSEREAU

Montreal, January 10, 1945.

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Phylogeny of Nearctic Sciuridae

Monroe D. Bryant¹

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Introduction

The aims of this investigation are: first, to determine the phylogenetic relationships of the Nearctic Sciuridae by study of the external features, the osteology, the myology, and the paleontology of representatives of the supra-specific groups; second, to summarize the data available on fossil sciurids; third, to discover the osteological and myological features which are of special adaptive significance; and, fourth, to prepare a selected list of synonyms for each muscle described.

The systematic position of the species of Nearctic squirrels is based principally on the cranial and external features. These features are well known in most of the squirrels, but since there is no agreement concerning their generic and subgeneric allocations, a more comprehensive study is required. With this requirement in mind, I have reviewed the work that has been done upon the cranial and external features of Nearctic squirrels and, in addition, have made a comparative study of the osteology and myology of representative forms and have examined most of the fossil sciurid material known from North America.

¹ (Contribution from the Museum of Vertebrate Zoology of the University of California).

Since the materials and methods vary with the several phases of the problem, they are indicated in their appropriate places in the text.

The system of classification followed is given on page 386. The terminology used is that of the international system (B. N. A.), or the English equivalents, except in those instances where these anatomical terms, for man, are misleading when applied to sciurids. The adverbial forms of the adjectives dorsal, ventral, anterior, posterior, and similar terms ending in "ally" denote position; those ending in "ad" indicate course, that is to say direction.

I wish to express my gratitude particularly to Professor E. Raymond Hall of the Museum of Vertebrate Zoology for guidance in the study and for critical assistance with the manuscript. Dr. R. A. Stirton of the Museum of Paleontology gave similar assistance with the section relating to fossil forms, and I am grateful also to Professors Alden H. Miller and Charles L. Camp for assistance. For the loan of essential fossil materials, I am indebted to Dr. J. LeRoy Kay of the Carnegie Museum, Professor Chester Stock of the California Institute of Technology, and Dr. Claude W. Hibbard of the University of Kansas. I am grateful also to Mr. Charles C. Sperry of the Denver Wildlife Research Laboratory, Mr. Louis E. Miller of the Colorado State Game Commission, and Messrs. Starker Leopold and Charles W. Schwartz of the Missouri Conservation Commission, for supplying preserved materials. The illustrations of fossil specimens were prepared by Mr. Owen Poe, and those of muscles and bones were made by Miss Viola Memmler. The drawings of the teeth (except fig. a of Pl. 2, and c and d of Pl. 6, by Memmler) were made under the direction of Dr. C. Hart Merriam, probably between 1890 and 1900, and were included in his gift, in 1941, of personal materials to the Museum of Vertebrate Zoology. All these drawings except those of specimens numbered 23853, 23902 and figs. a, b of Pl. 6 were checked by me for agreement with the specimens themselves.

External Features

The extensive collection of study skins in the Museum of Vertebrate Zoology, containing representatives of all supraspecific categories and of most of the species of Nearctic squirrels, was used in the study of the external features. The following alcoholic specimens were examined:

- Tamias (Neotamias) speciosus*, 11, Yosemite National Park, California.
- Marmota flaviventris*, 2, Yosemite National Park, California.
- Ammospermophilus interpres*, 5, Brewster Co., Texas.
- Ammospermophilus harrisi*, 5, Pima Co., Arizona.
- Ammospermophilus leucurus*, 8, San Bernardino and Kern counties, California.
- Ammospermophilus nelsoni*, 2, Fresno Co., California.
- Citellus (Otospermophilus) variegatus*, 5, Kerr and Brewster counties, Texas.
- Citellus (Otospermophilus) beecheyi*, 3, Tulare and Fresno counties, California.
- Citellus (Callospermophilus) lateralis*, 9 Yosemite National Park, California.
- Citellus (Citellus) beldingi*, 11, Yosemite National Park, California.
- Citellus (Xerospermophilus) tereticaudus*, 8, Pima Co., Arizona.
- Citellus (Xerospermophilus) mohavensis*, 1, San Bernardino Co., California.
- Citellus (Poliocitellus) franklinii*, 1, Sullivan Co., Missouri.
- Citellus (Ictidomys) mexicanus*, 11, Kerr Co., Texas.
- Citellus (Ictidomys) tridecemlineatus*, 10, Grayson Co., Texas.
- Cynomys gunnisoni*, 4, Park and Costillo counties, Colorado.
- Sciurus niger*, 2, Taney Co., Missouri, and Alameda Co., California.
- Tamiasciurus douglasii*, 2, Yosemite National Park and Eldorado Co., California.
- Glaucomys volans*, 1, Grayson Co., Texas.
- Glaucomys sabrinus*, 1, Wallowa Co., Oregon.

In the discussion of the external features, the subgenus *Otospermophilus* is taken as the standard; the other groups of Nearctic sciurids are compared with it. In these comparisons attention is called only to selected differences, including those judged to be indicative of relationships. If a group is not mentioned in the discussion of a character, it is understood that the group does not essentially differ from *Otospermophilus*. The following references contain comprehensive lists of external measurements of Nearctic sciurids: Allen, 1898; A. H. Howell, 1915, 1918, 1929, and 1938; Hollister, 1916. The data upon which are based the statements about the relative lengths of the limbs are given in table 2, pages 292-293.

Form of Body.—The body of *Otospermophilus* is of a generalized terrestrial form. The head and eyes are large, the ears are well developed, the neck is stout, the limbs are of medium length in comparison with those of other squirrels, the fore limbs are shorter and more mobile than the hind limbs, and the distichous tail comprises from one-third to one-half of the total length. In *Callospermophilus* the tail is about one-third of the total length. *Poliocitellus* appears to have relatively longer hind limbs, and the ears are short and rounded. *Ictidomys* is more nearly fossorial in form; the ears are short and rounded, the limbs are relatively shorter, and the tail-length is between one-fourth and one-half of the total length. The general proportions of the body in *Xerospermophilus* are similar to those in *Ictidomys*, but the ear is reduced to a thickened rim. Specialization for a fossorial existence is most pronounced in *Cynomys*, *Marmota*, and the subgenus *Citellus*. In these the ears are poorly developed, the limbs are relatively shorter than those of other sciurids, and the tail-length is less than one-third of the total length. In *Ammospermophilus* the ears are short and broad, the tail-length is between one-fourth and one-third of the total length, and the legs are relatively longer. Short ears and tail are characteristic of the semi-fossorial squirrels, but the presence of long legs parallels the condition in chipmunks and tree squirrels. The body of *Neotamias* is slenderer, the limbs are relatively longer except in comparison with those of *Ammospermophilus*, the ears are relatively longer, and the semi-bushy tail is from one-third to one-half of the total length. Chipmunks are semi-arboreal in form. *Sciurus* and *Tamiasciurus* resemble *Neotamias* in the general proportions of the body, but the tail is bushy and in *Sciurus* is relatively longer. The body of *Glaucomys* is slenderer, the ears are relatively larger and the legs relatively much longer than in other sciurids, and a broad fold of skin extends from the wrist to the ankle; the tail is broad and flattened and its length is almost one-half of the total length.

Color Pattern.—In *Otospermophilus* the back is mottled or variegated, except in completely melanistic individuals; the underparts are light in color. The color pattern of *Xerospermophilus*, *Cynomys*, and some species of the subgenus *Citellus* consists of pepper-and-salt upper parts and light-colored underparts. The upper parts of *Marmota* are grizzled or uniformly dark, except on parts of the head of some kinds. The upper parts of *Glaucomys* and most species of *Sciurus* are uniform in color and contrast sharply with the light underparts. Two species of *Ictidomys*, *C. spilosoma* and *C. perotensis*,

are irregularly spotted as in some species of the subgenus *Citellus*; but the other two species, *C. mexicanus* and *C. tridecemlineatus*, have stripes alternating with longitudinal rows of spots. The latter condition is not found in other Nearctic sciurids. A pattern of longitudinal stripes on a uniform or pepper-and-salt background occurs in *Ammospermophilus*, *Callospermophilus*, and *Tamias*. In *Ammospermophilus* a light stripe extends through the ground color on each side of the body from the shoulder to the hip or to the base of the tail. A similar pattern occurs in *Callospermophilus*, but the light stripes are bordered by black below and usually above. In *Tamiasciurus* and some species of *Sciurus* a dark stripe is present on each side of the body between the dark upper parts and light underparts. The most complicated pattern of stripes is present in *Tamias*, in which there are three dark and two light stripes on each side of the head and five dark and four light stripes on the dorsum of the body. The dorsal stripes extend from behind the occiput to or nearly to the rump. The two lateral light stripes are more nearly white than the two medial light stripes.

Vibrissae.—The vibrissae conform to the general rodent arrangement (Pocock, 1914). The mystachials vary from 12 to 23 in number, and the more posterior ones are the longest. A row of from 3 to 5 (usually 4) superciliary vibrissae extends dorsocaudad from the anterior angle of each eye. A vertical series of from 3 to 6 genals is present near the center of each cheek. The submentals are small or absent, and there are usually 2 interramal vibrissae. The carpal vibrissae are well developed. An ulnar vibrissa is present on the outer side of the forearm proximal to the carpus. *Marmota* has from 5 to 8 (usually 6) superciliary and from 3 to 6 large interramal vibrissae. *Sciurus* and *Tamiasciurus* have relatively longer mystachials and submentals and usually 3 long interramals. *Glaucomys* has relatively longer mystachials than does any other genus examined, 1 or 2 superciliaries, and no ulnar or interramal vibrissae. The greater development of the mystachials in the arboreal forms, and particularly in *Glaucomys*, is probably correlated with the need for greater tactile perception in these animals. Tactile vibrissae are present on the ventral surface of the body in tree squirrels.

Rhinarium.—The rhinarium is shallow, broad, and convex. The round nares open anterolaterally from under the margin of the septum and are partially separated from a lateral groove by a small dorsal fold. The nares and lateral groove in combination are comma-shaped. When the tip of the muzzle is drawn downward, the supranarial border covers the nares and the openings are reduced to convex slits. The rhinarium of *Neotamias* is relatively deeper and nearly circular, and the narial groove is shorter. In *Sciurus* the rhinarium is deeper, the supranarial border is nearly straight, and the septum is shorter and broader. In *Tamiasciurus* the rhinarium is deeper than in *Sciurus*. In all genera the upper lip is divided to a point below the nares, where the sides fuse to form a groove which continues upward on the septum to the supranarial border.

Eye.—The eyes of sciurids are large, and have a small, black-tipped plica semilunaris under the anterodorsal surface of the upper eyelid. They are relatively smallest in *Marmota* and largest in *Glaucomys*, in correlation with the

fossorial habits of the former and the nocturnal habits of the latter. The iris and pupil are round. The eye is surrounded by a light-colored ring in all forms except *Glaucomys*. In *Tamias* the ring is interrupted at the angles.

Ear.—The ears extend above the level of the head, are pointed at the apex, and are much higher than wide. The upper part of the auricula is separated from the cymba concha and conchal cavity by the antihelix. Its anterior border folds over from the apex or slightly in front of it and bends sharply posteriad, as the crus helices, below the anterior end of the antihelix and ends in an enlarged, hairy conchal lobe. The posterior margin of the auricula folds over and is thickened below the posterior end of the antihelix. There is no tragus and the antitragus is small or indistinguishable. The intertragal notch is shallow or absent. The ears of *Callospermophilus* resemble those of *Otospermophilus* more closely than do the ears of other ground squirrels. However, the conchal lobe is smaller and the intertragal notch is deep and narrow. In the other ground squirrels and in marmots and prairie dogs the ears are smaller, seemingly in correlation with the fossorial habits of these animals. The ears of *Marmota* project slightly above the level of the head and differ from those of *Otospermophilus* in having a shorter and relatively wider auricula. The ears of *Ictidomys*, subgenus *Citellus*, *Poliocitellus*, *Ammospermophilus*, and *Cynomys* do not project dorsally to the level of the head, the auricula is rounded and its width is equal to or greater than its height, and in the last three groups there is no antitragus or intertragal notch. The antitragus is small in *Ictidomys*; the intertragal notch is shallow. In the subgenus *Citellus* the antitragus and intertragal notch are present in some species and absent in others. The ears of *Xerospermophilus* are smaller than those of any other Nearctic squirrel; the auricula is reduced to an oval, thickened rim, and the antitragus and the intertragal notch are absent. The ears of chipmunks, tree squirrels, and flying squirrels are similar in general structure and differ in several respects from those of the previously mentioned forms. The auricula is large and extends well above the level of the head, is pointed at its posterodorsal margin, and is rounded in front and sharply emarginate behind. In *Sciurus*, *Tamiasciurus*, and *Tamias* the anterior margin of the auricula is folded over more than it is in *Otospermophilus*, the conchal lobe is smaller and the conchal cavity is consequently less occluded, a small tragus is present, the antitragus is larger, the intertragal notch is deep, and a fold of skin projects above the external auditory opening. As compared with *Sciurus*, the conchal lobe is smaller in *Tamiasciurus*, and the antitragus is a large movable lobe which folds into the space between the conchal lobe and tragus to close the lower part of the conchal cavity. In *Glaucomys* the auricula is membranous, the tragus and antitragus are small, the conchal lobe is very small, and the conchal cavity is inflated posteriorly and is relatively larger than in other squirrels. The latter condition probably results in increased sonic perception in correlation with the nocturnal activity of *Glaucomys*.

Manus.—The manus of Nearctic sciurids does not vary in general structure but exhibits wide adaptive differences in detail. In *Otospermophilus* it is stout and the metacarpus is but little longer than wide. There are five apical pads, three interdigital pads, and two metacarpal pads. The apical pad of the pollex

is the smallest. The radial, middle, and ulnar interdigital pads are situated at the bases of digits 2, 3 and 4, and 5, respectively. The thenar pad is larger and more distally situated than the hypothenar. Four digits are stout and bear heavy claws, but the pollex is vestigial. The pollex bears a flat nail in all sciurids except *Cynomys*, in which it terminates in a small claw. Digit 3 is the longest but digit 4 is almost as long. Digit 2 is shorter than 4 and longer than 5. Digits 3 and 4 are closely associated at their bases. The claws are heavy at the base, dorsally moderately curved, nearly flat on the proximal part of the ventral surface, and abruptly decurved at the tip when unworn. Those of digits 3 and 4 are the longest. The claws are relatively longer and slenderer in *Ictidomys*, *Ammospermophilus* (except *interpres*), *Xerospermophilus* (except *tereticaudus*), *Callospermophilus*, subgenus *Citellus*, and *Cynomys*. The manus of *Marmota* differs from that of *Otospermophilus* in its more massive form, relatively greater size of the pads, and stouter claws. The fore feet of *Tamias*, *Sciurus*, and *Tamiasciurus* are relatively longer and narrower than in the previously mentioned forms, and digit 4 is usually slightly longer than digit 3. The claws are deep at the base and are strongly arched on both dorsal and ventral surfaces so that the surfaces form arcs of relatively smaller circles than do those of terrestrial sciurids. The claws of *Tamias* are relatively smaller than those of other Nearctic sciurids except *Glaucomys*. In *Glaucomys* digits 3 and 4 are subequal, as are digits 2 and 5; the manus is relatively longer and weaker than in other squirrels; the claws are exceptionally deep at the base and are strongly compressed and arched.

Pes.—The stoutness of the pes, the relative lengths of the digits and the shape of the claws (except on digit 1) are the same as in the manus. The claw on digit 1 is well developed. The sole is thinly haired from the heel to the interdigital pads, but the hairs are often worn away. There are five apical pads and four interdigital pads; metatarsal pads are absent. The interdigital pads are located at the bases of digits 1, 2, 3 and 4, and 5. The five digits are long and stout. Digits 3 and 4 are closely associated at their base as in the manus. The movement of the hind feet is more restricted in terrestrial squirrels than in other kinds; the claws are shorter than those of the fore feet. In *Ammospermophilus* and *Xerospermophilus* the sole is heavily haired. There are two metatarsal pads in *Marmota*. *Sciurus* has the thenar pad and sometimes also the hypothenar. *Tamiasciurus* may have the thenar pad, or both metatarsal pads may be absent. The manus and pes of various sciurids have been described by Pocock (1923).

Mammae.—The number and position of the mammae in Nearctic squirrels is highly variable individually. There are from four to seven pairs in ground squirrels, with 2/2 pectoral, 2/2 abdominal, and 1/1 inguinal the most common arrangement. Of six specimens of *C. tridecemlineatus* examined, four had six pairs of mammae, one had six on one side and five on the other, and one had seven on one side and six on the other. *C. mexicanus*, in the same subgenus has four or five pairs of mammae. *Marmota* has four or five pairs; *Cynomys* four to six pairs; and *Sciurus*, *Tamiasciurus*, *Glaucomys*, and *Tamias* usually have four pairs, of which one is pectoral, two are abdominal, and one is inguinal.

Discussion.—The external features of squirrels, as of other mammals, have been subjected to the indirect molding influence of the environment to a greater extent than have other parts of the body. Consequently, it is impossible to distinguish between external characters which have broad phylogenetic significance, if there be any, and those that are cenotetic. The external features are certainly of value in differentiating between species, but it is doubtful that any external feature is of sufficient phylogenetic significance to warrant its use in differentiating between genera. It is true that one or more of these features can be used to characterize supraspecific groups, but it should be borne in mind that these groups are definable in an evolutionary sense on more fundamental characters and that the recognition of the groups on the basis of external features is of secondary importance.

On the basis of their external features, Nearctic squirrels are divisible into two groups: the flying squirrel group and the terrestrial squirrel, tree squirrel, and chipmunk group. The flying squirrels are characterized by the presence of a gliding membrane, the absence of ulnar vibrissae, the presence of one or two superciliary vibrissae, subequal third and fourth and subequal second and fifth digits, and distinctive shapes of the ears and claws. The terrestrial and tree squirrels and chipmunks lack a gliding membrane and have a common pattern of the vibrissae. They may also be divided into two groups. The marmots, prairie dogs, and ground squirrels are characterized by the following features: terrestrial or semi-fossorial form of body; ears and claws of distinctive shapes; and digits in order of increasing length 1-5-2-4-3. The chipmunks and tree squirrels are characterized as follows: semi-arboreal or arboreal form of body, ears and claws of distinctive shapes; and the digits in order of increasing length are 1-5-2-3-4 (3 and 4 may be subequal). Most of the genera and subgenera in each of these divisions are distinguishable only by a combination of several external characters. The color patterns of *Ammospermophilus*, *Callospermophilus*, and *Tamias* are distinctive.

Skeletal System

Complete skeletons of the following animals were examined:

- Tamias (Tamias) striatus*, 2, Long Island, New York.
Tamias (Neotamias) townsendii, 4, Siskiyou and Trinity counties, California.
Tamias (Neotamias) amoenus, 10, Adams Co., Idaho, and Elko Co., Nevada.
Marmota monax, 1, Douglas Co., Kansas.
Marmota flaviventris, 8, Fresno and Tuolumne counties, California, and Nye and Elko counties, Nevada.
Ammospermophilus leucurus, 5, San Bernardino and Kern counties, California, and Millard Co., Utah.
Ammospermophilus harrisi, 3, Yuma Co., Arizona.
Ammospermophilus nelsoni, 5, Merced Co., California.
Citellus (Otospermophilus) variegatus, 3, White Pine and Lander counties, Nevada.
Citellus (Otospermophilus) beecheyi, 9, Mendocino, Monterey, and Trinity counties, California.
Citellus (Otospermophilus) annulatus, 1, Compostela, Nayarit, Mexico.
Citellus (Callospermophilus) lateralis, 10, Shasta and Plumas counties, California, Wheeler Co., Oregon, and Elko Co., Nevada.
Citellus (Citellus) townsendii, 4, Millard Co., Utah, and Payette Co., Idaho.
Citellus (Citellus) richardsonii, 5, Manitoba and Saskatchewan, Canada, and Steele Co., North Dakota.

- Citellus (Citellus) beldingi*, 6, Tuolumne and Modoc counties, California.
Citellus (Citellus) armatus, 2, Cassia Co., Idaho.
Citellus (Citellus) columbianus, 10, Adams, Grant and Washington counties, Idaho.
Citellus (Citellus) parryi, 2, Point Hope, Alaska.
Citellus (Xerospermophilus) tereticaudus, 5, Imperial, Inyo and Riverside counties, California.
Citellus (Xerospermophilus) mohavensis, 4, Los Angeles and San Bernardino counties, California.
Citellus (Ictidomys) mexicanus, 3, Val Verde Co., Texas.
Citellus (Ictidomys) spilosoma, 2, Coconino Co., Arizona.
Cynomys ludovicianus, 3, Cochise Co., Arizona, and Lipscomb Co., Texas.
Sciurus griseus, 6, Mendocino and Sonoma counties, California.
Sciurus niger, 5, Douglas Co., Kansas, and Boone Co., Arkansas.
Sciurus aberti, 2, Coconino Co., Arizona, and Chihuahua, Mexico.
Sciurus carolinensis, 1, Boone Co., Arkansas.
Tamiasciurus hudsonicus, 5, Barkerville District, British Columbia, Washington Co., Idaho, and Grant Co., Oregon.
Tamiasciurus douglasii, 5, Mariposa, Placer and Tulare counties, California.
Glaucomyx sabrinus, 6, Placer, Tuolumne and Shasta counties, California.
 Unless otherwise indicated 10 skulls of each of the above mentioned species were examined. Skulls of the following species were also studied:
Tamias (Tamias) striatus, 6, Boone Co., Arkansas.
Citellus (Otospermophilus) annulatus, 8, Colimo and Manzanillo, Colimo, Mexico.
Citellus (Poliocitellus) franklinii, 3, Lancaster and Dodge counties, Nebraska, and Sherburne Co., Minnesota.
Citellus (Ictidomys) tridecemlineatus, 10, Carlton and Sherburne counties, Minnesota.
Glaucomyx volans, 5, Fairfax Co., Virginia.

Axial Skeleton

In the discussion of the parts of the skeleton other than the skull, *Otospermophilus* is taken as the standard and the skeletons of other groups of squirrels are compared with it. If a group is not mentioned in the discussion of a part of the skeleton, it is understood that in this part it does not differ significantly from *Otospermophilus*.

SKULL

(Figs. 1-42)

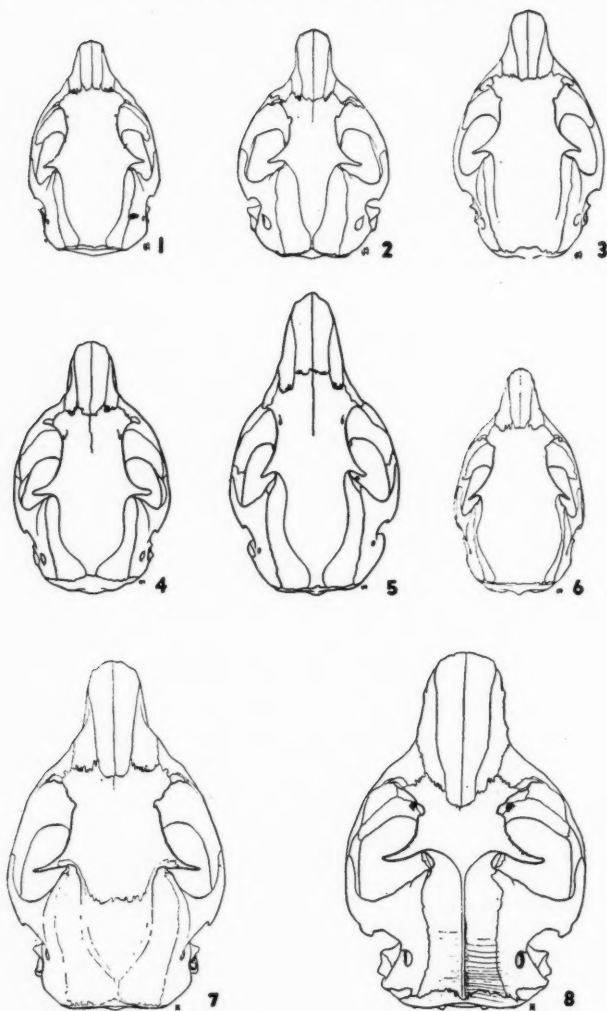
The general conformation of the sciurid skeleton has been adequately described (Weber, 1927:48-150, 1928:241-248), and a detailed description of the skeleton of *Sciurus vulgaris* is available (Hoffmann and Weyenbergh, 1870:3-37). Hall (1926:355-404) has reported upon the changes during growth in the skull of *Citellus (Otospermophilus) beecheyi*, and Hill (1935:121-129) has recorded his observations upon the cranial foramina of *Sciurus griseus* and *Citellus richardsonii*. These works, supplemented by others on restricted parts of the sciurid skull (Cockerell, Miller, and Printz, 1914; van Kampen, 1905), provide the information essential for a comparative study. Since additional purely descriptive material would be repetitive, the following discussion is limited to those features of the skull which differ supraspecifically.

Dorsal Profile.—The highest point of the moderately convex dorsal profile of the skull of ground squirrels, except *Ammospermophilus*, is situated slightly posterior to the plane of the postorbital processes. From this point to the

rostrum the skull is nearly flat. The downward inclination of the rostrum is approximately the same as that of the cranium posterior to the highest point. The dorsal surface slopes gradually downward in front of the highest point and lacks a bend at the base of the rostrum in *Tamias*, *Cynomys*, *Sciurus*, *Tamiasciurus*, and *Glaucomys*. In *Marmota* the dorsal profile is nearly flat.

Rostrum.—The rostrum of all Nearctic sciurids is short in comparison with the length of the skull, but it is relatively longer in *Poliocitellus*. Its depth and width are approximately the same in ground squirrels, marmots, prairie dogs, chipmunks, and flying squirrels; in tree squirrels the depth exceeds the width. The relatively greater depth of the rostrum in tree squirrels results from the greater depth of the upper incisor teeth, which is probably correlated with the resistant character of the food. The rostrum is expanded at the tip and constricted at the base in the subgenus *Citellus* and in *Cynomys*. It is more massive in *Marmota* than in other squirrels. The rostrum is relatively shorter in *Tamiasciurus* than in *Sciurus*, and in *Neotamias* than in the subgenus *Tamias*.

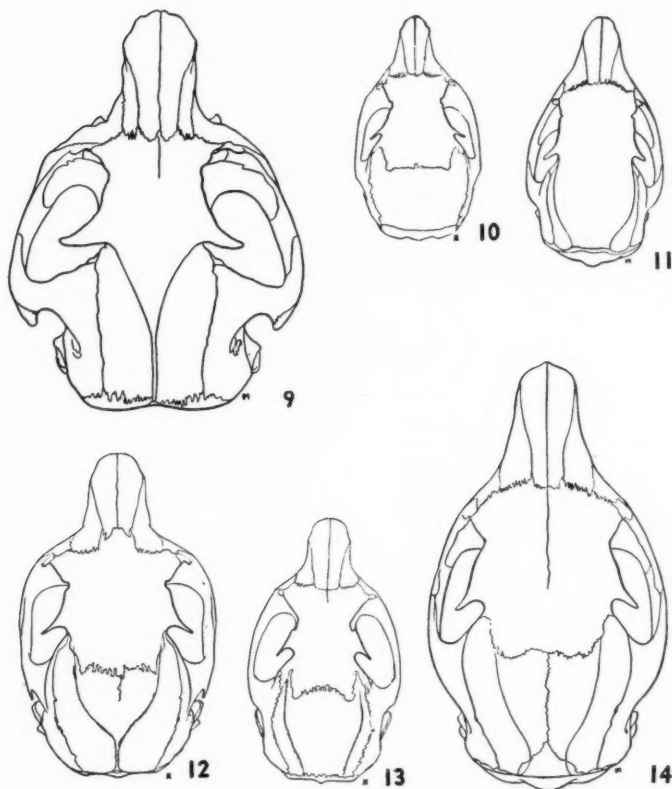
Cranium as a Whole.—Striking supraspecific differences are apparent in the conformation of the cranium. For the most part, these differences seem to be responses to the differential development of the parts of the brain. Although I have not studied the central nervous system of the squirrels, I feel that valuable data on the phylogenetic relationships of sciurids may be obtained by a study of this conservative system. The discussion here will be restricted to the broader features of the cranium; the detailed structure is considered in connection with the discussion of the bones composing the cranium. The cranium is shallow and weakly inflated in marmots and chipmunks. The inflation is greater in *Neotamias* than in the subgenus *Tamias*. In ground squirrels and prairie dogs the cranium is moderately inflated and of moderate depth. The inflation and depth are greater in tree squirrels than in chipmunks and terrestrial squirrels, and they attain their maximum in *Glaucomys*. From the dorsal view the cranium is ovate in *Poliocitellus*, *Otospermophilus*, *Callospermophilus*, *Sciurus*, *Tamiasciurus*, and *Glaucomys*; subglobular in *Cynomys*, *Marmota*, and subgenus *Citellus*; and nearly quadrate in *Ictidomys*, *Xerospermophilus*, and *Ammospermophilus*. The shape of the cranium as viewed from above depends upon the width at the postorbital constriction, the place of origin of the postorbital processes (see account of frontal bone on page 275), and the inclination of the posterior wall of the orbit. The postorbital constriction is narrow in the subgenus *Citellus*, *Poliocitellus*, *Cynomys*, *Marmota*, and *Glaucomys*, and is relatively broader in *Ictidomys*, *Otospermophilus*, *Xerospermophilus*, *Ammospermophilus*, *Callospermophilus*, and *Tamias*. It is much broader in *Sciurus* and *Tamiasciurus* than in other sciurids. The more nearly quadrate the cranium, the more nearly dorsal is the inclination of the posterior wall of the orbit. The groups listed in the order of decreasing inclination of the posterior part of the cranium from the highest point to the middorsal point of the superior nuchal line are: flying squirrels, tree squirrels, ground squirrels and chipmunks and prairie dogs, and marmots. The superior nuchal crest is strongly developed in the larger species of the subgenus *Citellus* and in



DORSAL VIEWS OF SKULLS (Natural size. Catalogue numbers, unless otherwise noted, are of the Museum of Vertebrate Zoology, University of California):

1. *Citellus (Xerospermophilus) tereticaudus*, ♀; no. 27381, Furnace Creek Ranch, Inyo Co., California.

2. *Citellus (Citellus) townsendii*, ♂; no. 41525, 6 mi. E Stillwater, Churchill Co., Nevada.



3. *Citellus (Callospermophilus) lateralis*, ♀; no. 45473, Kingston Ranger Station, Lander Co., Nevada.

4. *Citellus (Ictidomys) mexicanus*, ♀; no. 93789, 1/2 mi. NE Del Rio, Val Verde Co., Texas.

5. *Citellus (Poliocitellus) franklinii*, ♂; no. 192703, U. S. Nat. Mus., Biological Survey Collection, Elk River, Sherburne Co., Minnesota.

6. *Ammospermophilus leucurus*, ♂; no. 61472, 14 mi. E Searchlight, Clark Co., Nevada.

7. *Citellus (Otospermophilus) variegatus*, ♂; no. 41517, Baker Creek, White Pine Co., Nevada.

8. *Marmota flaviventer* ($\times 2/3$), ♂; no. 57476, Toquima Mtn., Nye Co., Nevada.

9. *Cynomys ludovicianus*, ♀; no. 44365, Higgins, Lipscomb Co., Texas.

10. *Tamias (Neotamias) dorsalis*, ♂; no. 47949, SW Base, Groom Baldy, Lincoln Co., Nevada.

11. *Tamias (Tamias) striatus*, ♂; no. 96863, 3 mi. SW Phoenicia, Ulster Co., New York.

12. *Tamiasciurus douglasii*, ♀; no. 65215, Incline Creek, Washoe Co., Nevada.

13. *Claucomys sabrinus*, ♂; no. 69640, Marlette Lake, Washoe Co., Nevada.

14. *Sciurus griseus*, ♂; no. 60026, French Gulch, Kern Co., California.

Cynomys and *Marmota*. The parietal ridges are prominent and meet at an acute angle well in front of the superior nuchal line in the subgenus *Citellus*, *Marmota*, and *Cynomys*; are prominent and meet at an acute angle shortly anterior to the crest in *Otospermophilus*; are obsolete, lyre-shaped, and either join or are adjacent at their junction with the line in *Poliocitellus*, *Ictidomys*, *Callospermophilus*, *Tamias*, *Sciurus*, *Tamiasciurus*, and *Glaucomys*; and are obsolete and broadly lyre-shaped in *Xerospermophilus* and *Ammospermophilus* (see account of temporalis muscle on page 309).

Premaxilla.—The frontal processes of the premaxillae are relatively broader in tree squirrels and chipmunks than in other Nearctic sciurids. This is correlated in the former with the greater width of the interorbital region and in the latter with the smaller size of the dorsal and lateral parts of the zygomatic plates. The incisors of tree squirrels are deep and narrow and do not produce prominent swellings on the sides of the premaxillae as they do in other sciurids. In *Marmota* the massive rostrum permits the passage of the heavy incisors without the formation of large external swellings on the premaxillae. In squirrels that possess cheek pouches (see account of cheek pouches on page 315) a small muscle runs from the anterodorsal part of each pouch to the part of the premaxilla posterior to the alveolus of the incisor and anterolateral to the incisive foramen. The place of origin is marked by a depression which is absent or small in the sciurids that do not possess cheek pouches. The size of this depression varies directly with the size of the pouch and the size of the animal. It is faintly indicated in *Xerospermophilus*, which consists of small animals with small pouches, and in *Marmota*, in which the pouches are rudimentary. This character has been of value in determining the relationships of some fossil squirrels. In tree squirrels the premaxillary-maxillary suture runs anteriad on the dorsal surface of the zygomatic plate, crosses the zygomatic crest, runs ventrad toward the masseteric tubercle to a point dorsal to the tubercle, and passes anteroventrad on the side of the rostrum to its junction with the incisive foramen. In other Nearctic sciurids this suture crosses the anterior tip of the zygomatic crest, runs ventrad well in front of the masseteric tubercle, and passes anteriad to the incisive foramen only after attaining the ventral surface of the rostrum.

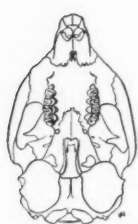
Maxilla.—The maxilla has been more profoundly altered in the course of evolution of the squirrels than any other bone of the skull. This is probably correlated with the variation occurring in the masseter muscle, particularly the superficial and the anterior parts of the masseter lateralis, as a result of diversified feeding activities. The differences in the shape of the anterior part of the lateral surface may be inferred from the discussion of the premaxillary-maxillary suture in the preceding paragraph.

The infraorbital foramina are oval or subtriangular in terrestrial and flying squirrels, and are anteroventrally slanting slits in tree squirrels. In *Otospermophilus*, *Ammospermophilus*, *Callospermophilus*, and *Glaucomys* the external margins of the foramina are usually vertical, the bases are directed ventrolaterad, and the masseteric tubercles are situated ventral or slightly ventrolat-

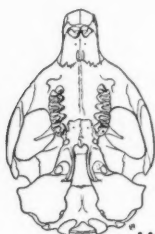
eral to the foramina. In the subgenus *Citellus*, *Poliocitellus*, *Ictidomys*, *Xeromorphophilus*, *Marmota*, and *Cynomys* the external margins usually slant ventrolaterad, the bases are horizontal, and the masseteric tubercles form pronounced elevations ventrolateral to the foramina. Since the superficial part of the masseter takes its origin from the masseteric tubercle, it is assumed that this muscle is stronger in the forms with larger masseteric tubercles. In any event, it is evident that the differences present in the region of the infraorbital foramen are largely dependent upon this muscle. In chipmunks the infraorbital foramen pierces the zygomatic plate and there is no infraorbital canal. The foramen is relatively larger than in other Nearctic squirrels, a condition probably resulting from the penetration of the foramen by the ventral head of the maxillonasalis muscle (see page 314); the masseteric tubercles are small. In tree squirrels the masseteric tubercles are less prominent than in other squirrels, except chipmunks, and have larger areas for the attachment of the superficial parts of the masseters, which have broad flat tendons in contradistinction to the cord-like tendons of other forms.

In terrestrial squirrels the fossa on the anterior surface of the zygomatic plate (masseteric fossa), upon which the masseter lateralis pars anterior originates, is narrow in relation to its length, is markedly convex, has a crest overhanging its lateral margin, and terminates anterodorsally in a definite depression posterior to the premaxillary-maxillary suture. In chipmunks the fossa is narrower and more acutely pointed anterodorsally than in other sciurids. The fossa is broad and slightly convex in tree and flying squirrels, and the dorsal margin terminates on the side of the premaxilla in tree squirrels. The depression at the dorsal end of the fossa is shallow in tree squirrels and flying squirrels. In terrestrial squirrels and chipmunks the crest overhanging the lateral margin of the dorsal part of the fossa has a projection anterior to the lacrimal foramen. The dorsal head of the maxillonasalis muscle arises on this projection. In tree and flying squirrels, which lack this head of the maxillonasalis, this projection is absent. The notches in the zygomatic plates are opposite M^1 in most sciurids but are opposite P^4 in subgenus *Tamias*, *Neotamias*, and *Glaucomys*, and are opposite the anterior edge of M^1 or posterior edge of P^4 in *Tamiasciurus*. The notches are farther forward in *Neotamias* than in *Tamias*. The zygomatic plate forms an angle of about 65° with the basicranial axis in *Glaucomys*, about 60° in *Sciurus* and *Tamiasciurus*, about 50° in *Citellus*, *Ammospermophilus*, *Marmota*, and *Cynomys*, and about 45° in *Tamias*. The jugal bone forms the lateral margin of the ventral half of the zygomatic plate in all squirrels. In addition it overlaps the maxilla in the ventrolateral part of the anterior surface of the plate and forms an integral part of the zygomatic notch in ground squirrels, prairie dogs, and marmots. In *Tamias* the extension of the jugal on the anterior surface of the plate is less than in the above mentioned forms, is still less in *Glaucomys* and *Tamiasciurus*, and is small or absent in *Sciurus*.

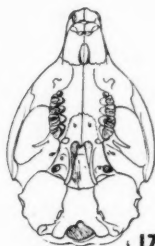
The alveolar borders of the maxillae are parallel in tree and flying squirrels and in chipmunks, slightly convergent posteriorly in ground squirrels and marmots, and markedly convergent posteriorly in prairie dogs. The shape



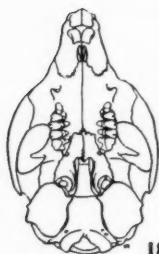
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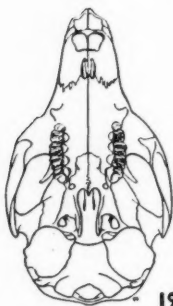
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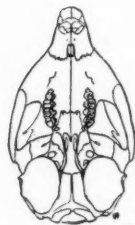
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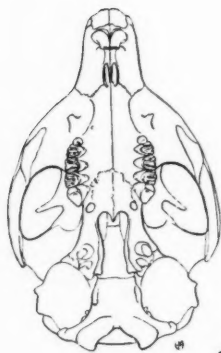
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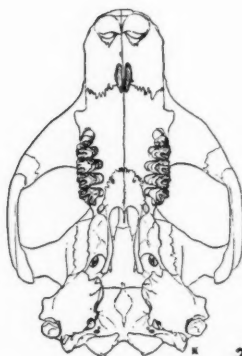
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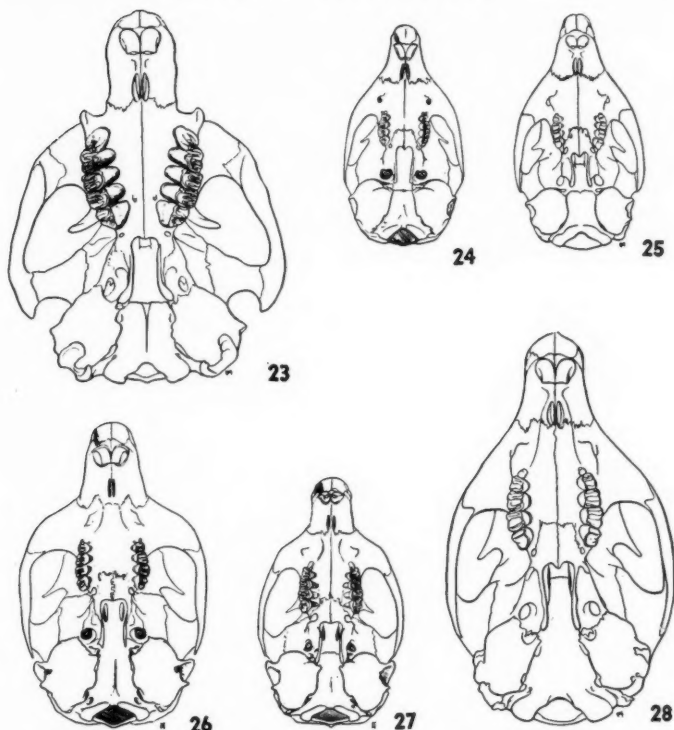


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VENTRAL VIEW OF SKULLS. (Natural size. Catalogue numbers, unless otherwise noted, are of the Museum of Vertebrate Zoology, University of California).

15. *Citellus (Xerospermophilus) tereticaudus*, ♀; no. 27381, Furnace Creek Ranch, Inyo Co., California.

16. *Citellus (Citellus) townsendii*, ♂; no. 41525, 6 mi. E Stillwater, Churchill Co., Nevada.



17. *Citellus (Callospermophilus) lateralis*, ♀; no. 45473, Kingston Ranger Station, Lander Co., Nevada.

18. *Citellus (Ictidomys) mexicanus*, ♀; no. 93789, 1/2 mi. NE Del Rio, Val Verde Co., Texas.

19. *Citellus (Poliocitellus) franklinii*, ♂; no. 192703, U. S. Nat. Mus., Biological Survey Collection, Elk River, Sherburne Co., Minnesota.

20. *Ammospermophilus leucurus*, ♂; no. 61472, 14 mi. E Searchlight, Clark Co., Nevada.

21. *Citellus (Otospermophilus) variegatus*, ♂; no. 41517, Baker Creek, White Pine Co., Nevada.

22. *Marmota flaviventris* ($\times 2/3$), ♂; no. 57476, Toquima Mtn., Nye Co., Nevada.

23. *Cynomys ludovicianus*, ♀; no. 44365, Higgins, Lipscomb Co., Texas.

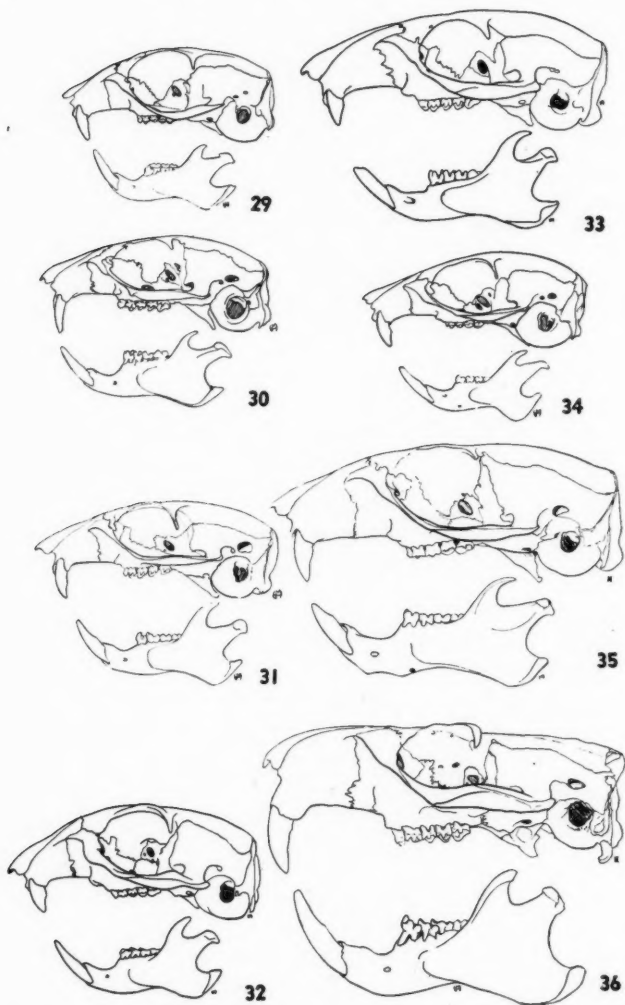
24. *Tamias (Neotamias) dorsalis*, ♂; no. 47949, SW Base, Groom Baldy, Lincoln Co., Nevada.

25. *Tamias (Tamias) striatus*, ♂; no. 96863, 3 mi. SW Phoenixia, Ulster Co., New York.

26. *Tamiasciurus douglasii*, ♀; no. 65215, Incline Creek, Washoe Co., Nevada.

27. *Glaucomys sabrinus*, ♂; no. 69640, Marlette Lake, Washoe Co., Nevada.

28. *Sciurus griseus*, ♂; no. 60026, French Gulch, Kern Co., California.



LATERAL VIEWS OF SKULLS. (Natural size. Catalogue numbers, unless otherwise noted, are of the Museum of Vertebrate Zoology, University of California).

29. *Citellus (Xerospermophilus) tereticaudus*, ♀; no. 27381, Furnace Creek Ranch, Inyo Co., California.

30. *Citellus (Citellus) townsendii* ♂; no. 41525, 6 mi. E. Stillwater, Churchill Co., Nevada.

of the palate varies in accordance with the direction of the alveolar borders. The palate of *Tamias* is relatively longer than that of *Neotamias*.

Jugal Bone and Zygomatic Arch.—Low and rounded frontal processes are present on the jugal bones of tree squirrels. The zygomatic arches are parallel and closely appressed in tree squirrels and chipmunks, convergent anteriorly and closely appressed in *Ammospermophilus* and *Glaucomys*, and convergent anteriorly and expanded posteriorly in other Nearctic sciurids. The arches are more closely appressed in *Tamiasciurus* than in *Sciurus*. These relations of the zygomatic arches are dependent upon three factors: the width of the zygomatic plates, the curvature of the zygomatic arches, and the position of the squamosal roots of the arches. In tree squirrels the squamosal roots slant anteroventrad and slightly laterad, the arches are slightly curved, and the zygomatic plates are broad. In chipmunks the zygomatic plates are narrower than in tree squirrels, and the squamosal roots are directed more nearly ventrad. The resemblance of the arches in these two groups consequently results from a combination of different factors. In *Ammospermophilus* and *Glaucomys* the squamosal roots resemble those of tree squirrels, but the zygomatic plates are narrower in the former and the arches are more curved in the latter. In *Citellus* and *Marmota* the arches are moderately curved, the zygomatic plates are narrow, and the squamosal roots are directed laterad and less ventrad than in the above mentioned forms. This accounts for the wide spread of the posterior ends and the anterior convergence of the zygomatic arches. In marmots the squamosal roots are nearly horizontal, and the arches are consequently more widely expanded posteriorly than in the ground squirrels. In prairie dogs the proximal ends of the squamosal roots are directed horizontally laterad and the distal ends slant posteroventrolaterad. This results in the widest posterior expansion and the greatest anterior convergence of the zygomatic arches occurring in Nearctic sciurids, with the exception of marmots. The zygomatic arches of the subgenus *Citellus* are more widely expanded than are those of other ground squirrels, and they are most closely appressed in *Ammospermophilus*. The sides of the zygomatic arches are nearly vertical in tree and flying squirrels whereas in other sciurids they are twisted by almost a quarter of a turn so that the originally internal surfaces face dorsomedially. The twisting of the arch appears to be the result of differences in origin and relative strength of the masseter lateralis pars posterior and the masseter medialis pars anterior in these two groups of squirrels (see account of masseter muscle on pages 308-309). In terrestrial squirrels and chip-

31. *Citellus (Callospermophilus) lateralis*, ♀; no. 45473, Kingston Ranger Station, Lander Co., Nevada.

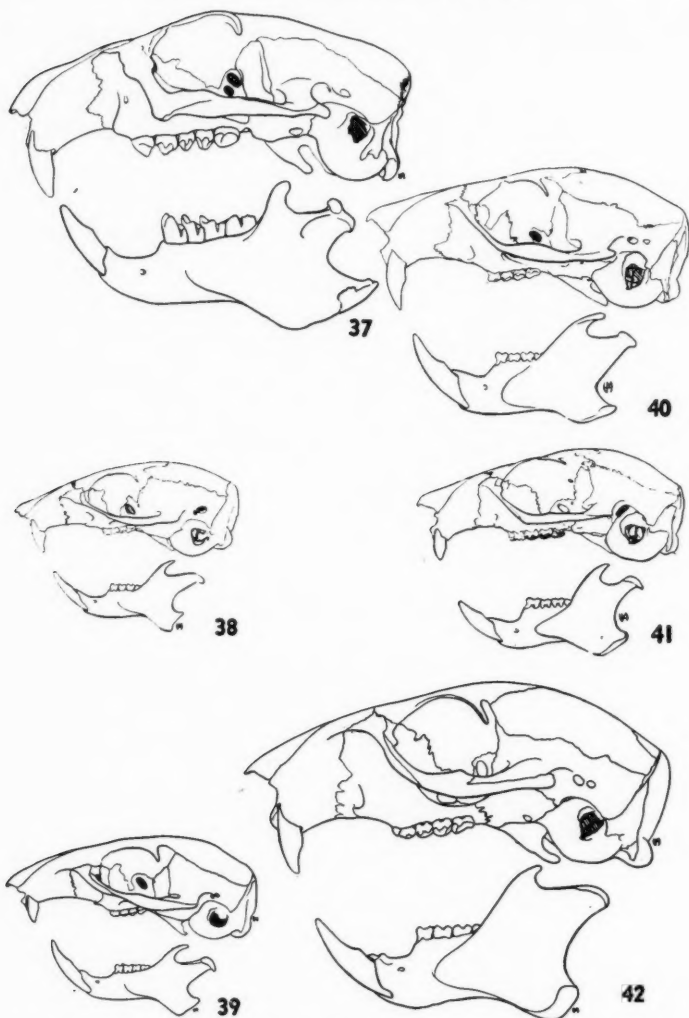
32. *Citellus (Ictidomys) mexicanus*, ♀; no. 93789, 1/2 mi. NE Del Rio, Val Verde Co., Texas.

33. *Citellus (Poliocitellus) franklinii*, ♂; no. 192703, U. S. Nat. Mus., Biological Survey Collection, Elk River, Sherburne Co., Minnesota.

34. *Ammospermophilus leucurus*, ♂; no. 61472, 14 mi. E Searchlight, Clark Co., Nevada.

35. *Citellus (Otospermophilus) variegatus*, ♂; no. 41517, Baker Creek, White Pine Co., Nevada.

36. *Marmota flaviventer* (×2/3), ♂; no. 57476, Toquima Mtn., Nye Co., Nevada.



37. *Cynomys ludovicianus*, ♀; no. 44365, Higgins, Lipscomb Co., Texas.
 38. *Tamias* (*Neotamias*) *dorsalis*, ♂; no. 47949, SW Base, Groom Baldy, Lincoln Co., Nevada.
 39. *Tamias* (*Tamias*) *striatus*, ♂; no. 96863, 3 mi. SW Phoenicia, Ulster Co., N.Y.
 40. *Tamiasciurus douglasii*, ♀; no. 65215, Incline Creek, Washoe Co., Nevada.
 41. *Glaucomys sabrinus*, ♂; no. 69640, Marlette Lake, Washoe Co., Nevada.
 42. *Sciurus griseus*, ♂; no. 60026, French Gulch, Kern Co., California.

munks the posterior part of the masseter lateralis arises in a fossa which occupies the entire outer surface of the zygomatic arch. The anterior end of this fossa is marked by a process, except in *Ammospermophilus* and *Tamias*. This process is exceptionally large in *Cynomys*. In tree and flying squirrels the origin is limited to a fossa occupying the ventral part of the zygomatic arch. The fossa is further limited near the squamosal root because of the narrowing of the arch posterior to the frontal process of the jugal in tree squirrels and the reduced size of the posterior end of the jugal in flying squirrels.

Frontal.—The interorbital region of the skull of tree squirrels is relatively much broader than that of other Nearctic squirrels. Among the latter, it is relatively broad in *Otospermophilus*, *Callospermophilus*, and *Tamias*, long and narrow in *Poliocitellus*, and moderately constricted in the other forms, except *Glaucomys*. In *Glaucomys* the interorbital region is greatly constricted because the supraorbital notches are large and deep, and the supraorbital crest is small. Supraorbital foramina are usually present in *Poliocitellus* and *Ictidomys*, are often present in *Tamias* and *Otospermophilus*, and are usually absent (supraorbital notches are present) in other sciurids. The supraorbital notches or foramina are situated anterior to the plane of the zygomatic notches in ground squirrels, prairie dogs and marmots, near this plane in chipmunks and tree squirrels, and posterior to this plane in flying squirrels. The notches are farther forward in *Tamias* than in *Neotamias*. Since the anterior ends of the bases of the postorbital processes terminate at the supraorbital notches or foramina, the bases of these processes are relatively longest in terrestrial squirrels and shortest in flying squirrels. The size of the postorbital processes varies widely depending on the kind of squirrel; but, in general, the processes are long and project ventrolaterad and slightly posteriad in ground squirrels and prairie dogs, are long and project laterad in marmots, are short and project ventrolaterad and slightly posteriad in chipmunks, and are short and project posteroventrolaterad in tree and flying squirrels. The processes proper arise farther posteriorly in *Ictidomys*, *Xerospermophilus*, *Ammospermophilus*, and *Callospermophilus*, than in other sciurids. The anterior cranial fossa is relatively larger in *Otospermophilus*, *Callospermophilus*, and *Tamias* than in other ground squirrels and marmots and prairie dogs. It is relatively much larger in tree- and flying squirrels than in other sciurids. The differences in interorbital width and in the part of the skull between the zygomatic plates appear to result from the differences in the size of the anterior cranial fossa, which in turn are correlated with the size of the olfactory part of the brain.

Occipital.—In *Marmota* the paroccipital processes project ventrad well below the level of the tympanic bullae, the basioccipital bone is concave ventrally and does not have a sagittal ridge, and the processes on the basioccipital medial to the tympanic bullae arise from the middle of the ventrolateral margins of the bone. In other Nearctic squirrels the paroccipital processes end ventrally at or above the level of the tympanic bullae, a sagittal ridge is present on the ventral surface of the basioccipital, and the processes medial to the tympanic bullae arise near the anterior ends of the ventrolateral margins of the basioccipital.

Temporal.—The postglenoid and subsquamosal foramina are usually separate in squirrels except marmots. Temporal foramina are usually present in tree and flying squirrels. The mastoidal portion of the temporal bone is more inflated in *Glaucomys* than in other sciurids, probably in correlation with the nocturnal habits and presumably more acute auditory perception of these squirrels. In Nearctic squirrels, except tree and flying squirrels, the apices of the pyramids of the petromastoid portions of the temporals are large and come into contact posterior to the hypophyseal fossa.

Sphenoid.—The hypophyseal fossa is a well-marked depression in many squirrels but is indistinct in marmots, chipmunks, and tree and flying squirrels. In *Marmota* the dorsal margins of the optic foramina are parallel, the sphenoid is unstricted between the foramina, and the optic groove is quadrate in outline. In *Otospermophilus*, *Callospermophilus*, *Tamias*, and *Glaucomys* the dorsal margins of the optic foramina are moderately concave medially, the anterior end of the sphenoid between the foramina is moderately constricted, and the optic groove is trapezoidal in outline. The conformation of this area in other ground squirrels and in prairie dogs is intermediate to that in *Marmota* and *Otospermophilus*; the dorsal margins of the foramina being parallel posteriorly and convergent anteriorly, the intervening sphenoid is narrow, and the optic groove is narrowly trapezoidal. In tree squirrels the dorsal margins of the optic foramina are more concave medially than in other squirrels, the intervening sphenoid is broader anteriorly than posteriorly, and the optic groove is trapezoidal but with the larger base at the anterior end rather than at the posterior end as in *Otospermophilus* and other forms. The jugum sphenoidale is relatively shorter in tree and flying squirrels than in other sciurids, in correlation with the larger size of the olfactory lobes of the brain. The interpterygoid fossa is relatively broader, the pterygoid fossae are relatively narrower, and the lateral pterygoid plates are relatively smaller in tree and flying squirrels and chipmunks than in other squirrels. The pterygoid and interpterygoid fossae are narrower in chipmunks than in the tree and flying squirrels. The sphenopalatine foramina are large in tree squirrels.

Mandible (Figs. 29-42).—In terrestrial squirrels and chipmunks the diastemal part of the mandible is slender, rounded laterally, concave above and below, and flattened medially. The alveolar border is level with or below the level of the anterior tip of the mandible. The anterior margin of the alveolar surface passes ventrad to join the diastemal part in a gradual curve, except in the subgenus *Citellus* and in *Marmota* and *Cynomys*. In these three groups this junction is almost at a right angle as a result of the greater depth of the body of the mandible. The body of the mandible is deeper and relatively shorter in tree squirrels than in other sciurids, and the alveolar border is well above the level of the anterior end of the mandible. These differences are due to the greater depth of the lower incisors, which is probably an adaptation to the resistant type of food. In *Glaucomys* the diastemal part of the mandible is relatively deeper than in terrestrial sciurids and chipmunks, and the alveolar border is slightly above the level of the anterior end of the mandible. The masseteric fossa extends forward on the lateral surface of the mandible to the

plane of the anterior margin of the first molar or slightly anterior thereto. Its ventral crest is more prominent than the dorsal crest. The deep and triangular inferior pterygoid fossa occupies the medial surface of the angle and is delimited by strong dorsal and ventral crests.

The coronoid process is relatively shorter in *Ammospermophilus*, *Xerospermophilus*, and *Tamias* than in other ground squirrels and marmots and prairie dogs; it is still shorter in flying squirrels and tree squirrels. It projects more nearly dorsad in *Marmota*, *Cynomys*, and the subgenus *Citellus* than in other terrestrial squirrels. The angular process is large and becomes more prominent with increasing age. In terrestrial squirrels it extends posteriad as a pointed process as far as does the condyloid process. A ridge which ends in an enlargement at the posterior tip of the process is present on the distal margin of the angle. The angular process of the subgenus *Citellus*, *Marmota*, and *Cynomys* projects farther posteriad than in other squirrels. The ventral mandibular incisure is deep and acutely arched in *Ictidomys*, *Xerospermophilus*, and *Ammospermophilus*, is shallow and weakly arched in *Marmota*, and is intermediate in the other terrestrial sciurids. The angular process of chipmunks is small, and the posterior process is reduced in size and does not extend as far posteriad as does the condyloid process. In *Glaucomys* *Tamiasciurus*, and *Sciurus* the posterior projection of the angular process is absent, the angle is progressively relatively shorter and the ventral mandibular incisure is less arched in the order named, and the ridge on the distal margin is not enlarged posteriorly. The mandibular tooth rows are nearly parallel in all sciurids except *Cynomys*, in which they are slightly convergent posteriorly.

TEETH

(Pls. 1-6)

The following skulls were examined in addition to the skulls listed on pages 266-267 and 270-271:

Tamias (*Tamias*) *striatus*, 5; *Tamias* (*Neotamias*) *townsendii*, 10; *Tamias* (*Neotamias*) *speciosus*, 10; *Ammospermophilus* *leucurus*, 10; *Ammospermophilus* *nelsoni*, 10; *Citellus* (*Otospermophilus*) *variegatus*, 10; *Citellus* (*Otospermophilus*) *beecheyi*, 10; *Citellus* (*Callospermophilus*) *lateralis*, 10; *Citellus* (*Citellus*) *townsendii*, 10; *Citellus* (*Citellus*) *richardsonii*, 10; *Citellus* (*Citellus*) *armatus*, 2; *Citellus* (*Citellus*) *washingtoni*, 2; *Citellus* (*Citellus*) *columbianus*, 10; *Citellus* (*Citellus*) *parryi*, 2; *Citellus* (*Xerospermophilus*) *tereticaudus*, 10; *Citellus* (*Xerospermophilus*) *mohavensis*, 10; *Citellus* (*Ictidomys*) *mexicanus*, 5; *Citellus* (*Ictidomys*) *spilosoma*, 5; *Citellus* (*Ictidomys*) *tridecemlineatus*, 5; *Cynomys* *ludovicianus*, 5; *Marmota* *flaviventris*, 4; *Marmota* *monax*, 1; *Sciurus* *niger*, 5; *Sciurus* *griseus*, 11; *Sciurus* *aberti*, 2; *Sciurus* *carolinensis*, 3; *Tamiasciurus* *hudsonicus*, 11; *Tamiasciurus* *douglasii*, 10; *Glaucomys* *sabrinus*, 10; *Glaucomys* *volans*, 11.

The dental formula of the Sciuridae is
$$\frac{1-0-2(1)-3}{1-0-1-3}$$
 (see table 1, page

286). The incisors grow from permanently open roots. Consequently, they continue to grow throughout the life of the animal and are smaller in young animals than in old ones. Except by wear the cheek teeth do not change in size and shape after the roots are closed. The front and a part of the sides of the incisors

are covered by enamel. The order of eruption of the teeth in *Citellus* (*Otospermophilus*) *beecheyi* (Hall, 1926:390) is as follows: upper and lower incisors, upper and lower fourth deciduous premolars, third deciduous premolar and first lower molar, first upper molar, second lower molar, second upper molar, third lower molar, third upper molar, permanent upper premolars, and permanent lower premolars. My incomplete observations indicate that the succession of teeth in all Nearctic sciurids is essentially the same as in *C. beecheyi*.

The terminology of the parts of the cheek teeth of squirrels is a subject of disagreement. The terminology used here is that proposed by Wood and Wilson (1936) for rodents, with necessary additions made for the teeth of sciurids. In the Scuridae there are two crests connecting the protoconid with the antero-lingual cusp of the lower molars. The relations of these cusps and transverse crests indicate that the anterior crest corresponds to the protoloph of the upper teeth and that the posterior crest corresponds to the metaloph. This condition would arise through the fusion of the paraconid and metaconid. The antero-lingual cusp would then be homologous to these two conic's and herein is called the parametaconid. These conclusions are based on the assumption that the rodent dental pattern has been derived from a tuberculo-sectorial arrangement. It is possible that the ancestral forms had only one lingual cusp on the anterior part of the lower molars and that the rodent pattern has not been derived from a tuberculo-sectorial pattern. The same terminology is applied to all of the molariform teeth.

The protoconid of P_4 fits into the anterior valley of P^4 , and the parametaconid fits between the protocone of P^4 and the posteromedial style of P^3 . The anterior part of P_4 fits between the cusps of P^3 and the protoloph of P^4 . The

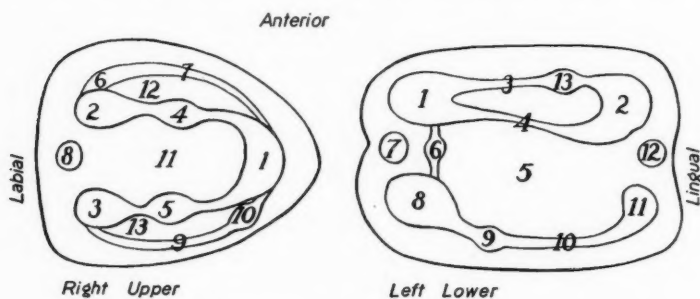


Fig. 43. Terminology of cheek teeth applied to sciurids

1, Protocone; 2, Paracone; 3, Metacone; 4, Protoconule on protoloph; 5, Metaconule on metaloph; 6, Parastyle; 7, Anterior cingulum; 8, Mesostyle; 9, Posterior cingulum; 10, Hypocone; 11, Central valley; 12, Anterior valley; 13, Posterior valley.

1, Protoconid; 2, Parametaconid; 3, Protolophid; 4, Metalophid; 5, Talonid basin; 6, Mesoconid on ectolophid; 7, Ectostylid; 8, Hypoconid; 9, Hypoconulid; 10, Posterolophid; 11, Entoconid; 12, Mesostylid; 13, Protoconulid.

trigonids of M_1 , M_2 , and M_3 occlude the anterior valleys of the corresponding upper teeth and thus shear against the posterior margins of the metalops of P^4 , M^1 , and M^2 and the anterior margins of the protoloph of M^1 , M^2 , and M^3 . The lingual part of the anterior cingulum is reduced in height. This allows the elongated parametaconids of the lower teeth to extend into the spaces between the protocones of the upper teeth. The hypoconids fit into the central valleys of the upper teeth and the protocones occlude the talonid basins of the lower teeth. The enlarged hypoconid of M_3 fits into the enlarged central and posterior valleys of M^3 .

Since the upper tooth rows are farther apart than the lower tooth rows, it is impossible for the two series to be in perfect occlusion at the same time. Nevertheless, the arrangement of the cusps is such that an excellent lateral grinding movement is assured. When the teeth are meshed the transverse ridges prevent a fore- and aft-movement of the mandible. When gnawing is desired this mechanical condition is overcome by lowering the mandible and pushing the lower incisors forward to make contact with the upper incisors. These relationships account for the fore and aft gnawing movements and the transverse grinding movements, which have greatly influenced the development of the masticatory muscles and the shape of the skull.

UPPER TEETH

Incisors.—Alveoli open cranioventrally in anterior ends of premaxillae. Incisors pass through lateral parts of premaxillae and maxillae and terminate medial to infra-orbital foramina. Upper incisors shorter, stouter, and more curved than lower ones; anterior surfaces usually more rounded than lateral surfaces; medial surfaces flat. In tree squirrels incisors relatively narrower and deeper than in other sciurids and more curved than in other forms except *Tamias*, *Ictidomys*, *Ammospermophilus*, and *Xerospermophilus*. Upper incisors slender, slightly curved, and procumbent in *Cynomys*, *Glaucomys*, and subgenus *Citellus*; slender, moderately curved, and perpendicular to basicranial axis in *Poliocitellus* and *Callospermophilus*; stout and moderately curved in *Otospermophilus* and *Marmota*. Enamelled surfaces of incisors of tree and flying squirrels usually finely crenulated; of marmots and chipmunks usually longitudinally grooved; and of ground squirrels and prairie dogs usually smooth.

Cheek Teeth.—The dental pattern and the shape of the cheek teeth of most of the supraspecific groups may be ascertained by an examination of Pls. 1-6. Only the characters that show significant supraspecific variation are discussed here. The cheek teeth are progressively larger from P^3 through M^3 , except in *Marmota*. P^4 is larger than M^1 in *Marmota flaviventer* and *Marmota caligata*, and these two teeth are approximately the same size in *Marmota monax*. P^3 is a simple, conical tooth. The protocone is the largest cusp on the molariform teeth. It always connects with the protoloph and the anterior and posterior cingula. The paracone and metacone are about the same size on all of the molariform teeth except M^3 , on which the metacone is small or absent. In prairie dogs the maxillary tooth rows are markedly convergent posteriorly and slant more laterad than in other sciurids. P^3 has one root. P^4 and the molars have three roots, of which the lingual one is the largest and the two labial ones are approximately equal in size.

The features of the molariform teeth which vary supraspecifically are: height of the crown, shape of the occlusal surface, width of the protocone,

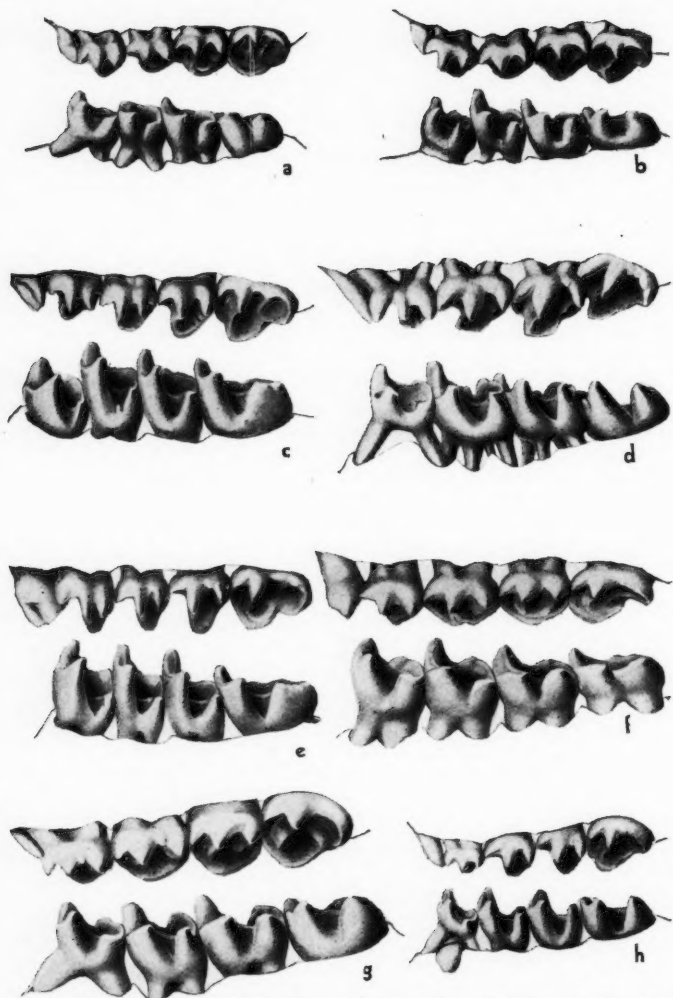


PLATE I.—Buccal views of left upper and lower cheek teeth ($\times 5$). a. *Citellus* (*Xerospermophilus*) *tereticaudus*, ♀; no. 23658, Phoenix, Maricopa Co., Arizona. b. *Citellus* (*Callospermophilus*) *lateralis*; no. 74069, Gold Hill, Boulder Co., Colorado. c. *Citellus* (*Citellus*) *richardsonii*, ♀; no. 55154, Bismarck, Burleigh Co., North Dakota. d. *Citellus* (*Poliocitellus*) *franklinii* (milk premolars), ♂; no. 48452, Ames, Dodge Co., Nebraska. e. *Citellus* (*Citellus*) *armatus*, ♀; no. 30153, Park City, Summit Co., Utah. f. *Citellus* (*Otospermophilus*) *annulatus*, ♂; no. 45589, Hda. San Antonio, Colima, Mexico. g. *Citellus* (*Otospermophilus*) *beecheyi* (milk premolars), ♂; no. 42658, Wawona, Mariposa Co., California. h. *Citellus* (*Citellus*) *townsendii* (milk premolars); no. 23853, Carson, Nevada.

(Catalogue numbers are of the United States National Museum, Biol. Surv. Coll.)

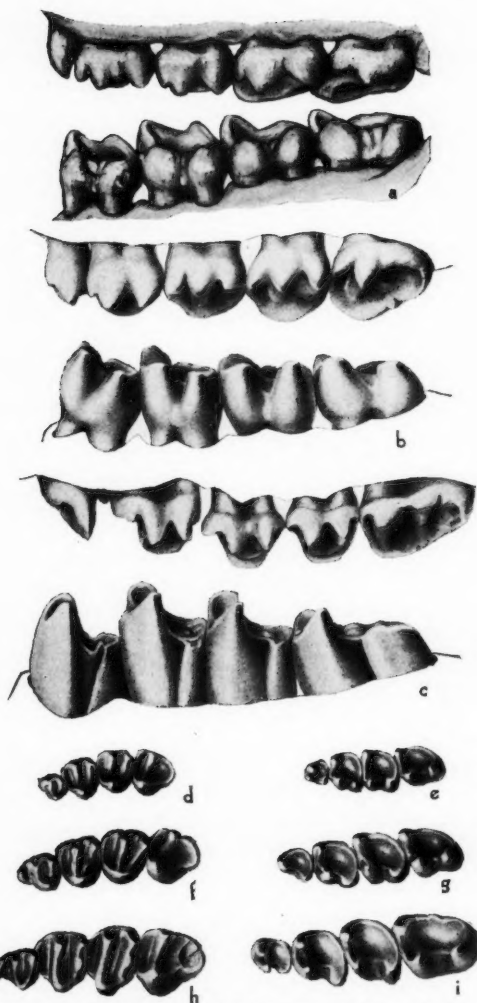


PLATE 2.—Figs. a-c. Buccal views of left upper and lower cheek teeth ($\times 5$). a. *Sciurus griseus*, δ ; no. 60026, Univ. Calif., Mus. Vert. Zool., French Gulch, Kern Co., California. b. *Citellus (Otospermophilus) variegatus*, δ ; no. 51282, Chihuahua, Chihuahua, Mexico. c. *Cynomys leucurus*, δ ; no. 55470, New Fork of Green River, Fremont Co., Wyoming.

Figs. d-i. Occlusal views of left upper and lower cheek teeth, with milk premolars ($\times 5$). d, e. *Tamias (Neotamias) minimus* (P3 present but not shown), \varnothing ; no. 74467, Estes Park, Larimer Co., Colorado. f, g. *Tamias (Tamias) striatus*, \varnothing ; no. 72838, Wilmington, Middlesex Co., Massachusetts. h, i. *Citellus (Citellus) townsendii*; no. 23853, Carson, Nevada.

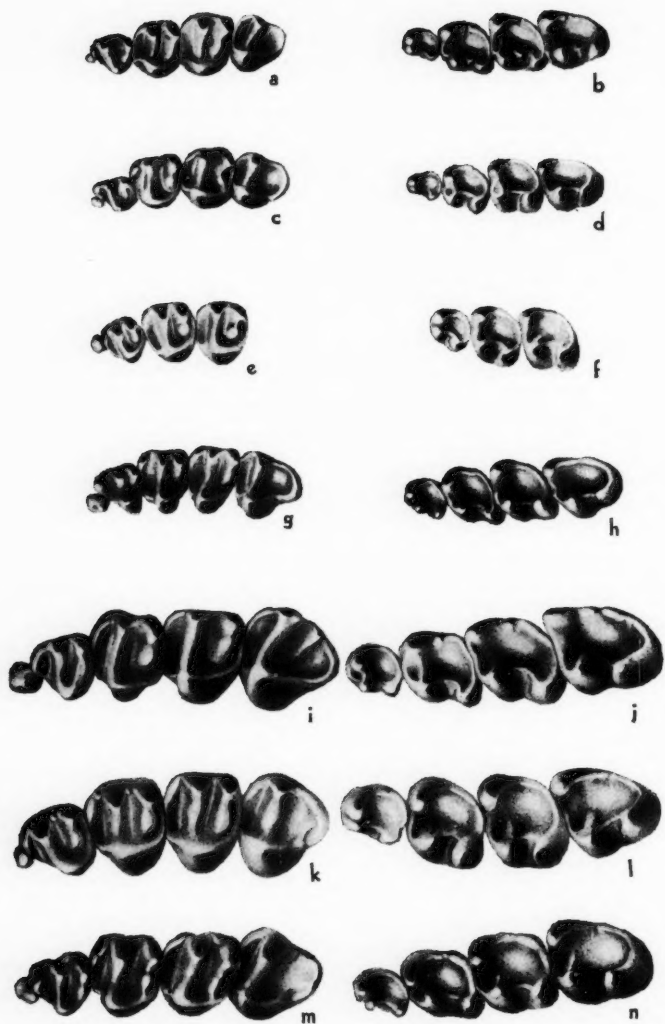


PLATE 3.—Occlusal view of left upper and lower cheek teeth, with milk premolars ($\times 5$). a, b. *Glaucomys volans*, ♀; no. 73761, Roan Mtn., North Carolina. c, d. *Ammodontomys leucurus*, ♂; no. 23902, Pyramid Lake, Washoe Co., Nevada. e, f. *Citellus (Xerospermophilus) tereticaudus*, ♀; no. 23659, Phoenix, Maricopa Co., Arizona. g, h. *Citellus (Ictidomys) tridecemlineatus*, ♂; no. 54444, Ellis, Ellis Co., Kansas. i, j. *Citellus (Citellus) parryi*, ♀; no. 42668, Unalaska, Alaska. k, l. *Citellus (Otospermophilus) beecheyi*, ♀; no. 41383, Kern River, California. m, n. *Citellus (Poliocitellus) franklinii*, ♂; no. 48452, Ames, Dodge Co., Nebraska.

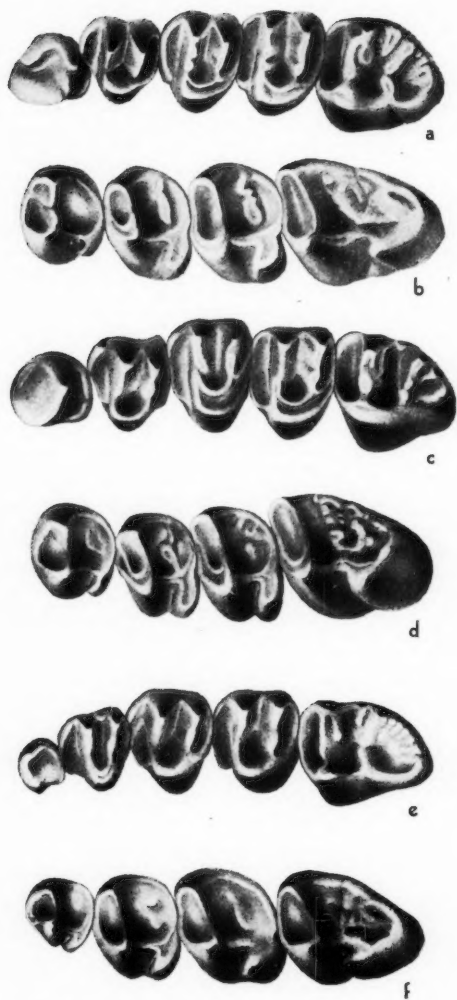


PLATE 4.—Occlusal views of left upper and lower cheek teeth ($\times 5$). a, b. *Cynomys gunnisoni*, ♂; no. 48159, Cochetope Pass, Saguache Co., Colorado. c, d. *Cynomys leucurus*, ♂; no. 55470, New Fork of Green River, Fremont Co., Wyoming. e, f. *Cynomys gunnisoni* (milk premolars), ♂; no. 47209, Fort Garland, Costilla Co., Colorado.

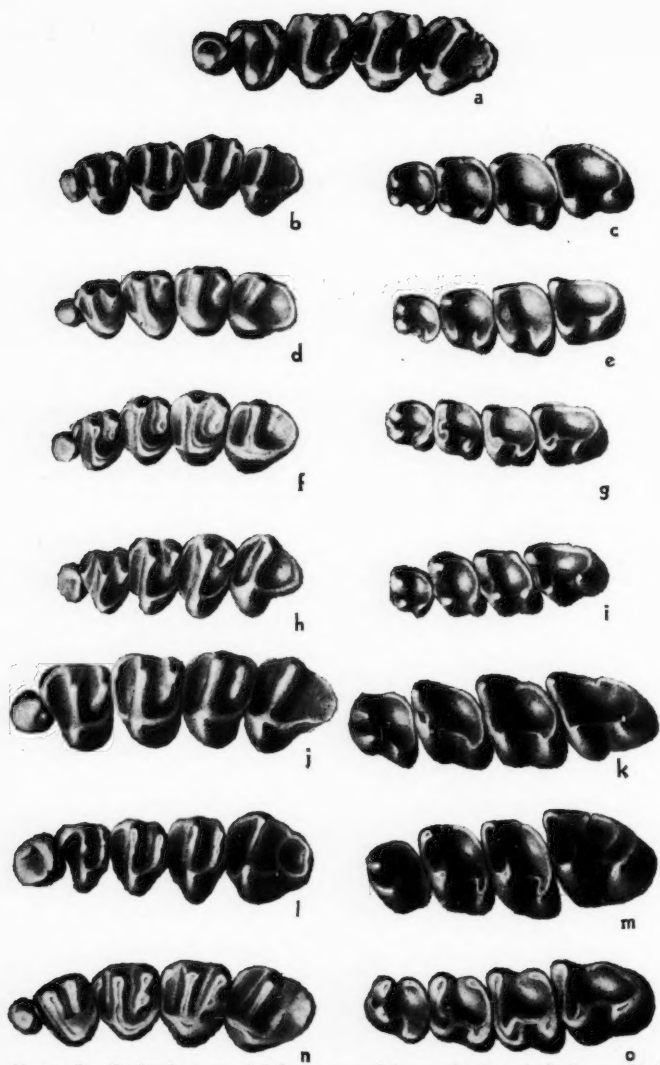


PLATE 5.—Occlusal views of left upper and lower cheek teeth ($\times 5$). a. *Citellus* (*Poliocitellus*) *franklinii*, δ ; no. 192703, Elk River, Sherburne Co., Minnesota. b, c. *Citellus* (*Callospermophilus*) *lateralis*; no. 74069, Gold Hill, Boulder Co., Colorado. d, e. *Citellus* (*Xerospermophilus*) *mohavensis*, \varnothing ; no. 40847, Salt Wells Valley, California. f, g. *Citellus* (*Xerospermophilus*) *tereticaudus*, \varnothing ; no. 23658, Phoenix, Maricopa Co., Arizona. h, i. *Citellus* (*Ictidomys*) *tridecemlineatus*, δ ; no. 47525, Cairo, Pratt Co., Kansas. j, k. *Citellus* (*Ictidomys*) *mexicanus*, δ ; no. 50096, Tlalpam, Mexico. l, m. *Citellus* (*Citellus*) *richardsonii*, \varnothing ; no. 55154, Bismarck, Burleigh Co., North Dakota. n, o. *Citellus* (*Otospermophilus*) *annulatus*, \varnothing ; no. 45232, Manzanillo, Mexico.

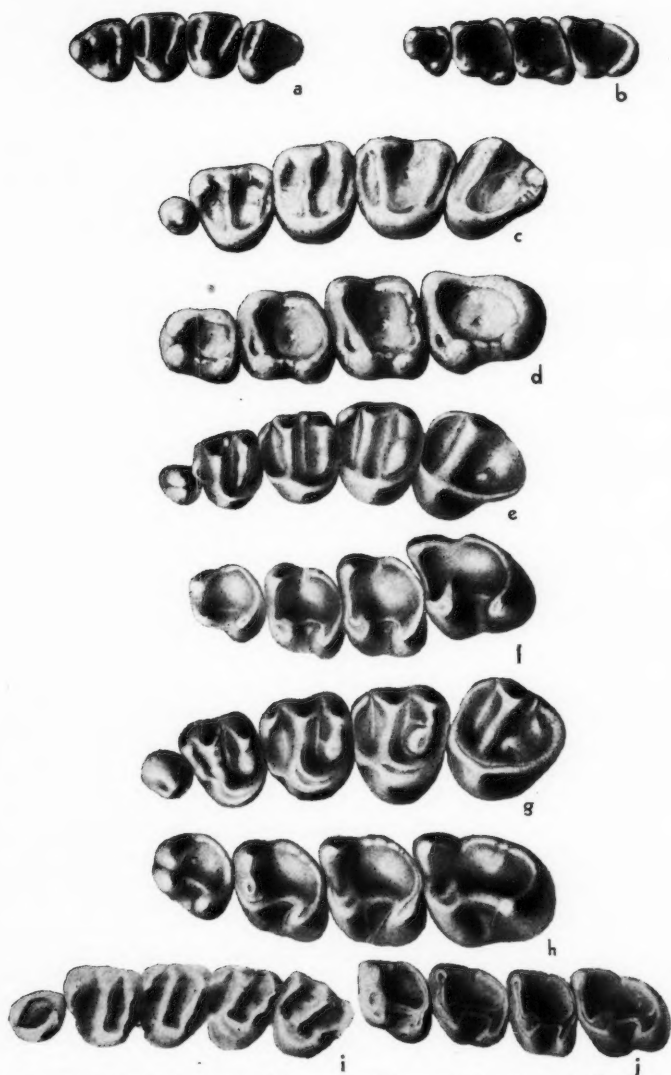


PLATE 6.—Occlusal views of left upper and lower cheek teeth. *a, b. Tamiasciurus douglasii* ($\times 5$)—unlabeled drawing. *c, d. Sciurus griseus*, δ ($\times 5$), no. 60026, Univ. Calif. Mus. Vert. Zool., French Gulch, Kern Co., California. *e, f. Citellus (Otospermophilus) beecheyi*, \varnothing ($\times 5$); no. 192655, San Francisco, San Francisco Co., California. *g, h. Citellus (Otospermophilus) variegatus*, \varnothing ($\times 5$), no. 45575, Zapatlan, Jalisco, Mexico. *i, j. Marmota caligata* ($\times 2\frac{1}{2}$); no. 42607, head of Cascade River, Skagit County, Washington.

height and position of the protoleph and metaloph, shape of the trigon, relation of the metaloph to the protocone, position of the metaconule in relation to the protocone and metacone, size and relation of the anterior cingulum to the protocone, relative height of the anterior and posterior cingula, relative size of the anterior and posterior valleys, size of the parastyle on P⁴, presence or absence of the mesostyles, and the size of M³ in comparison with the size of M². The differences in features which can be treated in tabular form are presented in table 1.

Third Premolar.—Circular or oval from occlusal view. *An oblique ridge with one cusp or two closely appressed cusps separates a minute anterolateral cingulum from a small posteromedial cingulum. Anteromedial end of oblique ridge reduced in size in *Marmota*, and anterior cingulum confluent with enlarged and often cuspidate posteromedial cingulum. P³ varies in size from a functional cutting tooth over one-half as large as P⁴ in *Cynomys* to a minute peg in chipmunks and tree squirrels; absent in some forms.

Fourth Premolar, First Molar, and Second Molar.—Height and sharpness of lophs, when unworn, vary directly with height of crown. Shape of outline of occlusal surface and shape of trigon of P⁴, M¹, and M² depend on width of protocone. If protocone is narrow, the cingula and lophs are sharply convergent toward the protocone, and occlusal surface and trigon are narrowly triangular and V-shaped, respectively. If protocone is nearly as broad as labial margin of tooth, the cingula are parallel and lophs are but slightly convergent; consequently occlusal surface is quadrate and trigon is U-shaped (see table 1).

TABLE 1.—Similarities and Differences in the Upper Cheek Teeth of Nearctic Sciurids.

	Size of P ³ 0—absent 1—smallest 6—largest	Ht. of Crowns of P ⁴ -M ³ 1—lowest 4—highest	Occlusal outline of M ¹ and M ² 1—narrowly triangular 2—subquadrate 3—quadrate	Trigon on P ⁴ -M ² 1—narrowly V-shaped 2—broadly V-shaped 3—U-shaped	Metaloph on P ⁴ , M ¹ , and M ² +—joins protocone —separated from protocone	Mesostyle on P ⁴ -M ² +—present —absent	Size of M ³ compared with M ² 1—slightly or no larger 4—greatest enlargement
<i>Cynomys</i>	6	4	1	1	+	+	4
<i>Marmota</i>	5	4	1	1	+	+	2
<i>Citellus</i>	5	4	1	1	+	—	3
<i>Ictidomys</i>	3	2	1+	1+	+	+	3
<i>Poliocitellus</i>	4	3	2	2	+	+	2-3
<i>Xerospermophilus</i>	2	2	2	2	—	—	2
<i>Otospermophilus</i>	3	2	2	2	—	+	2
<i>Ammospermophilus</i>	2	2	2	2	—	+	2
<i>Callospermophilus</i>	3	2	2	2	+	+	2
<i>Tamias</i>	0	2	2	2	+	+	2
<i>Neotamias</i>	1	2	2	2	+	+	2
<i>Sciurus</i>	0,1	1	3	3	+	+	1
<i>Tamiasciurus</i>	0,1	1	3	3	+	+	1
<i>Glaucomys</i>	2	2	3	3	+	—	1

a) Except on P⁴; b) Except in *C. parryi*; c) ± on P⁴.

There is a general correlation between the type of food eaten and the shape of the cheek teeth and the height of the crown. At one extreme, the graminivorous types, namely marmots and prairie dogs and members of the subgenus *Citellus*, have narrowly triangular teeth with high crowns and lophs; at the other extreme, the nut- and seed-eating tree squirrels have quadrate teeth with low crowns and ridges.

P4 is shaped like M_1 and M_2 in terrestrial squirrels. Anterior valley of P4 relatively is larger in *Marmota* than in other terrestrial sciurids. In tree and flying squirrels and chipmunks anterior cingulum short, consisting almost entirely of parastyle, and anterior valley limited to labial part of tooth; P4 consequently triangular in occlusal view, relatively longer than in other sciurids, and not shaped like M_1 and M_2 . There is a tendency toward fusion of metacone and metaconule on P4 of *Ictidomys*, *Ammospermophilus*, and *Xerospermophilus*.

Anterior cingulum of M_1 and M_2 joins protocone with abrupt change of direction in *Cynomys*, *Ictidomys*, and subgenus *Citellus*, and usually in *Xerospermophilus* and *Poliocitellus*. In *Otospermophilus*, *Ictidomys*, *Ammospermophilus*, *Xerospermophilus*, *Tamias*, and *Glaucomys* anterior cingulum slightly lower than posterior cingulum, which is almost as high as metaloph. Anterior cingulum much lower in comparison with height of lophs in *Cynomys*, *Marmota*, and subgenus *Citellus*. Cingula nearly on level with lophs in *Sciurus* and *Tamiasciurus*. Anterior valley always larger than posterior valley; anterior valley relatively larger in *Poliocitellus* and *Cynomys* than in other sciurids.

Third molar.—The features which differ supraspecifically are: relative size, relation of posterior cingulum to protocone, size and position of metaloph, and character of floor of basin. Anterior part of M_3 , including the protoloph, not appreciably different from corresponding part of M_2 . For difference in size of M_3 in comparison with size of M_2 see table 1. These differences are due to variation in size of posterior part of tooth. Posterior cingulum bends sharply posteriad from protocone in subgenus *Citellus*, *Ictidomys*, *Cynomys*, and *Tamias*, and curves gradually posteriad in other squirrels. Metaloph indistinct or absent in tree squirrels, flying squirrels, chipmunks, and ground squirrels (except subgenus *Citellus*); joins protocone but is lower than protoloph in *Cynomys*, *Marmota*, and subgenus *Citellus*. In *Marmota* metaloph turns posteriad to join posterior cingulum; consequently, central valley is large and posterior valley small. In *Cynomys* a ridge, not present in other sciurids, extends mediad from lateral margin posterior to protoloph or from posterolateral margin of protoloph; enamel folds arise from posterior cingulum and extend into basin of M_3 .

LOWER TEETH (Pls. 1—6)

Incisor.—Longer, slenderer, and less curved than upper incisors. Relatively deeper and more compressed in tree squirrels than in other sciurids; relatively wider in *Marmota*. Each incisor extends posteriad through ventral part of body of mandible and terminates at base of condyloid process; small tubercle on lateral surface of ramus marks point of termination.

Fourth premolar.—Temporary P4 smaller than permanent P4, but has approximately same dental pattern. It has two longitudinally flaring roots. Permanent P4 molariform in *Cynomys*, *Marmota*, and subgenus *Citellus*; occlusal surface shaped like a parallelogram; width greater than length. Occlusal surface trapezoidal in other sciurids; length equal to or greater than width. Differences in shape of occlusal surfaces due to varying distances between protoconid and parametaconid. In subgenus *Citellus*, *Cynomys*, and *Marmota* these conids are well apart, are connected by a long metalophid, and trigonid is nearly as broad as talonid. In other sciurids protoconid and parametaconid are close together, metalophid is short or absent, and trigonid is narrower than talonid; protoconid and parametaconid in contact in *Ammospermophilus* and *Tamias*; farther

apart in *Poliocitellus* and *Ictidomys* than in sciurids other than *Cynomys*, subgenus *Citellus*, and *Marmota*. Protolophid in *Cynomys* extends from protoconid to parametaconid and with metalophid encloses a small valley; in subgenus *Citellus* it extends obliquely ventromedial from protoconid to base of parametaconid, from which it is separated by small notch; in *Poliocitellus* and *Marmota* a transverse crest, seemingly homologous with protolophid, extends between the bases of protoconid and parametaconid and encloses a small depression; protolophid small and extends ventromedial from protoconid in *Ictidomys* and *Glaucomys*; small or absent in *Callospermophilus* and *Xerospermophilus*; usually absent in *Otospermophilus*, *Ammospermophilus*, *Tamias*, *Sciurus*, and *Tamiasciurus*.

Protoconid much larger than hypoconid in subgenus *Citellus* and *Cynomys*; these conids approximately equal in size in other sciurids. Talonid basin wider than long in subgenus *Citellus*, in *Cynomys*, and some species of *Ictidomys*.

First and Second Molars.—Occlusal surface and talonid basin parallelogram-shaped in *Cynomys*, *Marmota*, and subgenus *Citellus*; wider than long. Nearly rhomboidal in shape in other squirrels. Trigonid much higher than talonid in subgenus *Citellus* and *Cynomys*, about the same height as talonid in tree squirrels, slightly higher than talonid in *Tamias* and *Glaucomys*, and intermediate in height between *Cynomys* and *Tamias* in other forms. Depth of talonid basin in direct ratio to height of trigonid in comparison with height of talonid. Floor of talonid basin rugose in tree squirrels and has a highly variable pattern of enamel ridges in prairie dogs.

Protolophid complete in all sciurids. In chipmunks and flying squirrels protolophid has a narrow connection with the protoconid and also connects with anterior cingulum; a narrow groove present between protoconid and ridge to cingulum. In *Sciurus* protolophid joins metalophid about midway between protoconid and parametaconid; one ridge continues from this point to parametaconid. Metalophid extends from protoconid to parametaconid on M_1 and M_2 in subgenus *Citellus* and in *Cynomys*; encloses with protolophid a deep central valley, which does not communicate with talonid basin until metalophid is extremely worn. Metalophid joins protoconid and parametaconid on M_1 and is interrupted on M_2 in *Ictidomys*, *Poliocitellus*, *Ammospermophilus*, *Tamias*, and *Tamiasciurus*; low on M_1 and wears down early in life. Metalophid interrupted on M_1 and M_2 in *Otospermophilus*, *Xerospermophilus*, *Callospermophilus*, *Marmota*, and *Glaucomys*. Ectolophids nearly marginal in tree squirrels and slightly less marginal in chipmunks and flying squirrels, more medially located in *Cynomys* and *Marmota* than in other sciurids.

Mesoconid rarely present in *Otospermophilus*; present in chipmunks, tree squirrels, and flying squirrels and usually bilobed in tree squirrels. In tree squirrels hypoconid larger than protoconid and entoconid distinct.

THIRD MOLAR. M_3 largest of lower teeth; longer than wide in all sciurids but relatively shorter in tree squirrels. Trigonid differs from that of M_2 only in chipmunks, in which there is no ridge from anterior cingulum to protolophid. Talonid large in comparison with that of M_2 ; most enlarged in *Cynomys* and least enlarged in *Sciurus* and *Tamiasciurus*. Mesoconid present in chipmunks, tree squirrels and flying squirrels. Complicated enamel folds present in talonid basin of *Cynomys*, and small rugosities present in talonid basin of tree squirrels. Rounded protuberances are of sporadic occurrence in talonid basin of M_3 of other sciurids.

Discussion.—The significant phylogenetic differences apparent in the skulls of sciurids are principally associated with the masticatory mechanism and with the differential development of the parts of the brain. The facial and occipital muscles have played a minor role in inducing changes in the skull. The parts of the skull significantly modified are the rostrum, premaxillary-maxillary suture, area of the infraorbital foramen, zygomatic plate and arch, interorbital and sphenoidal regions, and mandible. As determined by a comparative study of these parts, there are three divisions of Nearctic sciurids: flying squirrels,

tree squirrels, and chipmunks and terrestrial squirrels. There is no intergradation in many of the characters that distinguish the chipmunks from the terrestrial squirrels, and it is certain that the separation of these two phyletic lines occurred at an early stage in the evolution of squirrels. Flying squirrels share some of the significant characters with each of the other two groups, but more with the tree squirrels than with the chipmunks and terrestrial squirrels. The differences apparent in the skulls of *Sciurus* and *Tamiasciurus* do not appear to warrant generic recognition of these two groups.

The upper cheek teeth exhibit a greater diversity of structure than do the lower cheek teeth. The presence or absence of P^3 has been considered of sufficient phylogenetic importance to warrant the separation of the Nearctic chipmunks into the genera *Tamias* and *Eutamias*. Since there is a tendency toward the disappearance of P^3 in most of the Sciuridae, as in other families of rodents, and since P^3 is occasionally absent in *Ammospermophilus*, *Neotamias*, and *Tamiasciurus*, and is absent in *Sciurus niger* among the tree squirrels, it appears that the establishment of genera on the basis of the absence of P^3 is unwarranted.

A comparison of the structure of the cheek teeth of Nearctic sciurids shows that there are three general plans. One type is found in ground squirrels, marmots, prairie dogs, and chipmunks; another is present in tree squirrels; and the third type characterizes flying squirrels. Chipmunks have more features of the teeth in common with tree squirrels and with flying squirrels than either the tree or flying squirrels have in common with other sciurids. The chipmunks, therefore, have teeth which in form occupy an intermediate position among the squirrels.

VERTEBRAL COLUMN

Cervical Vertebrae.—Atlas. Ventral arch narrower, deeper, and shorter than dorsal arch. Ventral tubercle on caudal border, for attachment of longus colli muscle, blunt and short; longer and sharply pointed in *Ammospermophilus*, *Neotamias*, *Glaucomys*, *Sciurus*, and *Tamiasciurus*; usually bifid in *Sciurus*. Dorsal arch biconvex; dorsal tubercle usually low and rounded. Cranial articular surfaces irregularly oval and moderately concave. Caudal articular surfaces circular and slightly concave; smaller than cranial articular surfaces and closer together. Transverse processes flattened, pointed caudally; relatively larger in terrestrial sciurids but never broadly expanded. Lateral masses heavy; transverse foramen penetrates lateral wall, and canal passes caudad lateral to caudal articular surface. In terrestrial squirrels outer wall of vertebral canal slants dorsolaterad from process ventral to posterior end of canal; outer wall relatively stouter, is directed horizontally and then turns vertically at right angle, and has no spine in *Tamias*, *Sciurus*, *Tamiasciurus*, and *Glaucomys*. Atlantal foramen at cranio-lateral angle of dorsal arch connects with foramen for first cervical nerve in ventro-lateral part of transverse process.

Axis.—Odontoid process subcylindrical; width slightly greater than depth, about one-half as long as centrum. Ventral articular surface continuous with cranial articular surfaces, which are concave dorsomedially, broadly rounded laterally, and convex cranially. Dorsal surface of centrum flattened; ventral surface slightly concave transversely; caudal face broadly oval and slightly concave. Y-shaped transverse processes small, directed caudad; base encloses transverse canal. Laminae in subgenus *Citellus*, *Cynomys*, and *Marmota* relatively longer than in other squirrels. Spinous process large, compressed. Caudal projection of spinous process long in subgenus *Citellus*, *Otospermophilus*, *Callospermophilus*, and *Marmota*, reaching nearly to caudal margin of third cervical vertebra; reduced in *Ictidomys*, *Ammospermophilus*, and *Xerospermophilus*; of

medium length in *Tamias*, *Sciurus*, *Tamiasciurus*, and *Glaucomys*; often bifid in tree squirrels.

The last five cervical vertebrae much alike. Centra wider than long; cranial surfaces weakly convex transversely and caudal surfaces slightly concave. Radicles short and stout. Cranial and caudal articular surfaces large and with contiguous bases. Laminae thin. Spinous processes rudimentary, usually longest on third cervical vertebra. Vertebral foramina semicircular, relatively narrower and deeper in terrestrial squirrels. Transverse foramina progressively larger in third through sixth vertebrae; absent in seventh vertebra in *Ictidomys*, *Ammospermophilus*, *Xerospermophilus*, and *Tamias*; usually absent in *Sciurus* and *Tamiasciurus*; present or absent in other ground squirrels and *Glaucomys*; usually present in *Marmota* and *Cynomys*. Costal parts of transverse processes proper are often absent on seventh vertebra (see transverse foramina above). On third through seventh vertebrae dorsal arches progressively shorter, centra progressively wider, and transverse processes progressively longer. Transverse processes directed caudolaterad on third, fourth, and fifth vertebrae; directed laterad on sixth and seventh. On third vertebra transverse processes proper terminate in sharp points, and separate minute costal processes are present lateral to transverse foramina; costal and transverse elements slightly more separated on fourth vertebra and transverse processes flattened laterally; on fifth vertebra costal processes longer than on fourth; ventral longitudinal ridges with well developed cranial and caudal processes on sixth vertebra.

Thoracic Vertebrae.—One specimen of *Citellus tereticaudus* has 13 thoracic vertebrae; other specimens examined have 12. First vertebra transitional in structure between cervical and thoracic regions; more like seventh cervical but centrum more convex transversely, articular surfaces flatter, vertebral foramen smaller, transverse processes shorter and stouter, cranial articular surfaces arise from bases of transverse processes, and spinous process well developed.

Centra increase in length throughout thoracic series. Wider on first and second vertebrae than on third through seventh, increase in width from eighth through twelfth. Increase in depth from ninth through twelfth. Slightly concave dorsally in last four vertebrae. Ventral surfaces of all except first and second vertebrae markedly convex in transverse axis and concave in longitudinal axis (saddle-shaped). Two foramina on dorsal surface.

Costal elements of transverse processes absent. Transverse processes proper stout and undivided on first and second vertebrae, divided into dorsal and ventral parts on third through ninth or tenth, ventral part absent on tenth or eleventh and twelfth; dorsal part progressively larger and ventral part smaller. Dorsal part consists of a process (accessory process) extending laterocaudad on third through sixth vertebrae, divided into accessory processes and cranially directed mamillary processes on seventh through tenth or eleventh. Mamillary processes fuse with dorsolateral margin of cranial articular processes on tenth or eleventh and twelfth, thus resembling lumbar vertebrae. Transverse processes arise on level with centrum on first, slightly above centrum on second, and slightly below level of dorsal part of vertebral canal on other thoracic vertebrae.

Vertebral foramina progressively smaller through third vertebra, about same size through tenth, and larger on last two vertebrae; size correlated with cervical and lumbar enlargements and intermediate constriction of spinal cord.

Cranial articular surfaces progressively higher on neural arches to sixth vertebra, slightly below level of dorsal margin of vertebral canal through tenth, and slightly above this level on eleventh and twelfth. Caudal articular surfaces far apart on first vertebra as on cervicals, closer together and higher on laminae on second and third, close together and arising at caudolateral bases of spinous processes on other thoracic vertebrae, enlarged on last two vertebrae.

Spinous processes vertical or inclined dorsocranial on first, progressively directed more caudad to tenth, nearly vertical on tenth, and directed cranial on eleventh and twelfth; those on last three or four vertebrae often fused. First spinous process low and slender, second through fifth long and slender, progressively shorter and stouter from sixth through twelfth. Relatively longer and slenderer in *Sciurus* and *Tamiasciurus*.

Cranial costal demifacet larger than caudal, both located ventral to caudal part of intervertebral canal. No caudal facets on last two vertebrae.

Lumbar Vertebrae.—Seven lumbar vertebrae present. Lumbar vertebrae longer than thoracic vertebrae and similar to last three thoracics. Centra shaped like those on thoracic vertebrae; those of first and seventh lumbar shorter than the subequal intermediate vertebrae. Cranial articular processes longer and mamillary processes more prominent in tree and flying squirrels than in other forms. Accessory processes large on first vertebra, diminish in size to fifth or sixth and usually absent on seventh; longer and slenderer in tree squirrels.

Transverse processes arise from craniodorsolateral surfaces of centra; flat, directed cranioventrolaterad. First process small. Processes increase in length and width through sixth vertebra. Shorter and wider in *Xerospermophilus*, but those of the subgenus *Citellus*, *Ictidomys*, and *Cynomys* of the same type; longer and narrower in other ground squirrels and *Tamias* than in previously mentioned forms; very long and narrow in tree squirrels and directed more nearly craniad than in the above forms; in *Glaucomys* directed craniad as in tree squirrels but small and inclined more nearly ventrad than in other sciurids.

Spinous processes progressively increase in height from the first through seventh vertebra; flat dorsally, directed craniad. Long on fourth to seventh vertebra in tree and flying squirrels; short in other genera. Vertebral foramina decrease in height from cranial to caudal end of region.

Sacral Vertebrae.—Sacrum composed of three vertebrae in *Tamias*, *Sciurus*, *Tamiasciurus*, and *Glaucomys*; in *Marmota* and *Cynomys* four vertebrae present. The following percentages of ground squirrels examined have four sacra: 55% in subgenus *Citellus*, 100% in *Ictidomys*, 71% in *Otospermophilus*, 75% in *Ammospermophilus*, 60% in *Xerospermophilus*, and 60% in *Callospermophilus*. The last lumbar is included in the sacral complex in one specimen of *Tamias amoenus* and one of *Citellus richardsonii*. Fourth vertebra, when present, not completely fused with other three.

First sacral vertebra larger than last lumbar, second and third progressively smaller. Vertebral canal in sacrum more depressed than in lumbar region. Transverse processes of first vertebra massive, lateral margins in complete articulation with ilia. Cranio-lateral margins of transverse processes of second vertebra stout; usually take part in pelvic articulation in ground squirrels and chipmunks, more broadly articulated in *Marmota* and *Cynomys*, not greatly enlarged and rarely included in pelvic articulation in tree and flying squirrels. All transverse processes fuse to form lateral mass. Cranial articular processes of first sacral like those of last lumbar vertebra; smaller on second and third sacra. Caudal articular processes small and close together; those of first and second vertebrae completely fused with cranial articular processes of second and third vertebrae. Part of sacrum between pelvic articulations more massive in ground squirrels and marmots than in other sciurids. Ventral surfaces of transverse processes of second vertebra nearly on level with those of first vertebra in ground squirrels, marmots, prairie dogs, and flying squirrels, but transverse processes higher and sagittal ridge on ventral surface of centrum more prominent in chipmunks and tree squirrels. First spinous process lower than second and third, except in *Glaucomys* and occasionally in *Marmota*; short in terrestrial squirrels and chipmunks and usually rudimentary in tree squirrels. Second and third spinous processes slenderer in tree squirrels than in other forms.

Fourth sacral is an extra bone and not first caudal fused into sacral complex, since the following vertebra is comparable in structure to first caudal of squirrels with only three sacra. Similar to third sacral but caudal parts of transverse processes are expanded into caudolateral projections.

Caudal vertebrae.—Number individually variable but there is a general correlation between length of tail and number of vertebrae. Number 15-21 in subgenus *Citellus*, 21-22 in *Ictidomys*, 21-22 in *Otospermophilus*, 19-20 in *Ammospermophilus*, 17-19 in *Xerospermophilus*, 18-20 in *Callospermophilus*, 18-20 in *Cynomys*, 22-24 in *Tamiasciurus*, 25-26 in *Sciurus*, and 21 in *Glaucomys*.

Centra gradually increase in length to tenth or eleventh vertebra and decrease in

TABLE 2.—Ratios of Parts of the Skeleton in Sciurids in Percentages (ratios of measurements are of length, unless otherwise stated).²

Catalogue no.	cervical vertebrae	thoracic vertebrae	vertebral column	lumbar vertebrae	vertebral column	scapula	vertebral column	width of scapula	humerus	vertebral column	radius	vertebral column	humerus + radius	olecranon	ulna	os coxae	vertebral column	femur	vertebral column	fibula	vertebral column	femur + fibula	sternum	vertebral column
Subgenus <i>Citellus</i>																								
<i>C. townsendii idahoensis</i>	67288	12.8	38.4	38.4	10.3	16.4	10.3	54.7	21.0	18.7	52.9	18.7	52.9	14.7	24.8	26.2	26.2	26.2	26.2	26.2	50.0	24.0	24.0	24.0
<i>C. townsendii mollis</i>	78476	12.9	40.0	36.9	10.2	15.9	10.2	57.0	22.1	19.3	53.6	19.3	53.6	15.6	26.2	26.2	26.2	26.2	26.2	27.5	49.1	
<i>C. townsendii mollis</i>	78479	12.3	37.3	38.6	11.6	16.7	11.6	54.3	21.9	18.6	55.0	18.6	55.0	16.2	26.2	26.3	26.5	26.3	26.8	49.4	
<i>C. richardsonii richardsonii</i>	54557	12.7	38.8	38.1	10.3	15.8	10.3	56.7	20.8	17.7	54.0	17.7	54.0	16.5	24.7	25.3	26.6	26.6	26.6	48.8	22.5	22.5	22.5	
<i>C. richardsonii richardsonii</i>	54558	13.2	38.8	37.8	10.2	15.7	10.2	60.3	19.8	17.5	53.0	17.5	53.0	15.8	23.6	24.1	25.9	24.1	25.9	48.2	23.2	23.2	23.2	
<i>C. richardsonii richardsonii</i>	81665	13.1	38.8	37.5	10.7	15.8	10.7	56.7	19.7	17.4	53.0	17.4	53.0	17.6	23.1	24.5	25.4	24.5	25.4	49.2	22.1	22.1	22.1	
<i>C. arnatus</i>	72124	13.2	39.4	37.0	10.4	16.6	10.4	56.9	21.1	53.2	53.2	17.2	25.4	25.4	25.4	25.4	25.8	49.2	22.1	22.1	22.1	
<i>C. beldingi oregonus</i>	12650	13.8	39.1	36.8	10.4	16.1	10.4	53.5	21.2	17.6	53.2	17.6	53.2	17.2	25.9	25.0	25.8	25.0	25.8	49.2	23.4	23.4	23.4	
<i>C. columbianus columbianus</i>	83640	13.2	38.0	37.2	11.6	17.0	11.6	57.2	21.4	17.3	55.1	17.3	55.1	17.1	25.9	25.4	27.4	25.4	27.4	48.6	23.2	23.2	23.2	
<i>C. columbianus columbianus</i>	83644	13.5	38.6	37.4	10.5	16.5	10.5	56.8	20.0	16.5	54.8	16.5	54.8	18.1	25.3	24.6	25.9	24.6	25.9	48.7	24.6	24.6	24.6	
<i>C. columbianus columbianus</i>	46793	14.0	38.1	36.9	11.0	16.3	11.0	58.6	21.2	17.1	55.4	17.1	55.4	17.8	25.8	26.4	27.7	26.4	27.7	48.7	23.0	23.0	23.0	
<i>C. columbianus columbianus</i>	83641	13.1	38.7	37.6	10.6	15.8	10.6	55.9	20.6	55.0	55.0	17.7	23.8	25.2	26.2	25.2	26.2	49.0	22.3	22.3	22.3	
<i>C. columbianus columbianus</i>	83642	13.4	39.4	37.2	10.3	20.7	16.8	55.0	16.8	55.0	17.7	25.5	25.9	26.3	25.9	26.3	49.6	
<i>Ictidomys</i>																								
<i>C. mexicanus parvidens</i>	93789	13.7	39.5	36.7	10.1	16.8	10.1	55.9	20.8	18.8	52.5	18.8	52.5	13.6	24.8	26.0	27.6	26.0	27.6	48.5	25.1	25.1	25.1	
<i>Xerospermophilus</i>																								
<i>C. tereticaudus tereticaudus</i>	10722	14.5	40.3	34.6	10.7	16.4	10.7	56.2	22.4	19.4	53.5	19.4	53.5	15.2	24.9	27.2	28.3	27.2	28.3	49.0	22.8	22.8	22.8	
<i>C. tereticaudus tereticaudus</i>	64802	14.1	38.3	35.6	12.1	16.7	12.1	60.2	23.2	55.2	55.2	15.6	25.2	27.5	27.5	27.5	27.5	49.1	21.1	21.1	21.1	
<i>C. mohavensis</i>	44285	14.2	39.7	34.8	11.7	16.6	11.7	53.8	22.4	18.7	54.5	18.7	54.5	15.6	25.8	26.7	27.2	26.7	27.2	49.1	21.1	21.1	21.1	
<i>Otospermophilus</i>																								
<i>C. variegatus grammurus</i>	78417	14.6	39.0	35.7	10.7	17.9	10.7	56.8	24.4	21.1	53.6	21.1	53.6	15.0	28.3	30.4	30.4	30.4	30.4	50.0	28.9	28.9	28.9	
<i>C. variegatus grammurus</i>	52215	14.5	39.5	35.6	10.4	16.9	10.4	53.5	19.3	54.6	19.3	54.6	16.1	27.4	29.4	29.4	29.4	29.3	50.0	
<i>C. variegatus grammurus</i>	88070	15.4	38.1	34.8	11.6	19.0	11.6	57.8	24.1	20.0	54.6	20.0	54.6	16.1	29.3	29.4	31.0	29.4	31.0	48.7	

Subgenus *Citellus**Ictidomys**Xerospermophilus**Otospermophilus**Callospermophilus**C. lateralis chondrodes*

Callospermophilus

C. lateralis chrysoideus.....	36632	13.3	40.4	35.8	10.7	18.0	50.7	22.8	19.3	54.2	17.1	26.1	29.0	29.7	49.4	22.7
C. lateralis chrysoideus.....	36629	13.8	38.4	36.8	10.9	18.6	48.2	23.4	19.5	54.5	16.2	28.1	30.2	30.3	50.0	25.5
C. lateralis chrysoideus.....	83610	14.7	39.3	35.2	11.0	18.9	50.5	24.8	21.4	53.6	15.8	29.5	31.9	33.2	48.9	24.5

Ammospermophilus

A. leucurus leucurus.....	78504	14.5	39.4	35.5	10.7	18.7	49.1	24.6	22.1	52.7	14.4	28.3	30.7	34.8	46.8	25.6
A. interpres.....	93797	14.6	39.5	35.0	11.0	18.3	48.6	24.7	21.9	53.0	14.6	30.1	31.0	32.7	48.7	28.3
A. interpres.....	93796	14.4	39.2	36.0	10.6	18.4	48.9	24.1	22.0	52.3	14.5	28.4	30.8	33.0	48.3	28.0

Cynomys

C. ludovicianus ludovicianus.....	44365	14.5	39.0	35.0	11.5	17.2	53.9	21.8	19.4	53.0	17.6	25.4	25.1	26.2	48.9	23.2
C. ludovicianus artizonensis.....	50305	14.6	38.9	35.7	10.8	17.3	55.2	22.5	19.5	53.6	25.9	26.1	26.1	50.0	24.0

Marmota

M. monax bunkeri.....	81778	17.8	36.6	34.6	10.8	16.8	66.0	23.6	19.0	55.3	19.2	27.6	27.5	27.0	50.4	22.9
M. flaviventris parvula.....	57476	17.3	37.7	35.2	10.0	19.3	53.3	22.9	18.2	55.7	19.3	27.4	27.2	24.5	52.5

Neotamias

T. townsendii senex.....	36645	13.5	38.1	36.0	12.4	18.3	51.2	24.8	22.5	52.4	14.2	28.9	32.1	34.5	48.2	24.7
T. townsendii senex.....	36647	13.3	37.9	36.8	12.0	18.2	49.7	24.5	22.8	51.7	13.4	28.2	32.1	34.3	47.3	25.6
T. townsendii senex.....	36646	14.6	38.0	35.1	12.4	18.5	49.1	23.8	22.3	51.7	14.3	27.4	31.7	35.3	47.3	22.5

Sciurus

S. griseus griseus.....	20738	13.0	37.4	37.0	12.6	17.2	56.0	24.8	23.0	51.9	14.8	28.6	33.2	38.3	46.4	26.9
S. niger rufiventris.....	38944	13.6	38.0	35.5	12.8	17.2	53.4	25.4	23.5	51.9	14.5	27.6	33.5	37.3	47.3	27.2
S. niger rufiventris.....	90636	13.7	37.6	36.1	12.7	17.5	55.6	25.1	23.8	51.3	13.5	29.3	33.1	36.0	48.6	27.4
S. aberti aberti.....	81643	13.8	38.7	36.2	11.3	16.8	52.2	24.6	22.5	52.2	13.7	26.7	31.8	34.9	47.6	24.4
S. aberti barberi.....	74859	14.0	37.9	35.8	12.3	16.9	57.7	24.5	23.3	51.2	14.0	27.7	32.1	35.6	47.4	27.0
S. carolinensis carolinensis.....	90630	14.0	38.3	35.3	12.3	17.4	54.8	24.8	22.6	52.3	13.3	28.5	33.4	36.1	48.1	26.3

Tamiasciurus

T. douglasii albolimbatus.....	19544	15.0	38.1	35.0	11.9	17.1	54.9	25.3	23.4	52.0	12.3	27.5	32.4	36.6	46.9
T. douglasii albolimbatus.....	37520	13.8	38.2	36.3	11.9	17.5	55.0	25.1	21.7	53.6	14.2	27.7	31.0	34.3	47.4	27.2
T. ludsonicus richardsoni.....	46801	13.8	37.6	36.4	12.2	17.9	56.2	25.5	21.9	53.8	15.0	27.8	32.2	36.0	47.2	30.5
T. ludsonicus richardsoni.....	83697	13.3	39.0	35.6	12.1	17.5	49.2	23.4	21.4	52.2	14.7	26.7	30.2	34.2	46.9	29.0

Glaucomys

G. sabrinus lasurus.....	34148	13.4	36.3	38.4	11.9	16.3	51.3	29.7	33.4	47.1	8.1	25.9	35.3	40.3	46.1	17.7
G. sabrinus lasurus.....	37480	12.1	36.9	39.4	11.6	16.8	50.7	30.3	33.2	47.7	8.7	27.3	34.1	38.8	47.1	17.9

² For footnote see page 294.

length thereafter. Vertebral canal tapers to end in seventh or eighth vertebrae. Cranial articular processes gradually decrease in size from cranial to caudal end of series. Caudal articular processes decrease in size from first through fifth to seventh vertebrae and are absent thereafter. V-shaped chevron bones present below articulations of first six to eight vertebrae, after which there is a small bone on each side of articulation.

Transverse processes usually divided into cranial and caudal parts by incisures on seventh caudal vertebra of *Otospermophilus*, *Sciurus*, and *Ictidomys*; usually divided on fifth or sixth in other sciurids. Judging from the comparative structure of the vertebrae it appears that fourth and/or fifth are lost in subgenus *Citellus*, *Xerospermophilus*, and *Glaucomyx* and that the fifth is often lost in *Callospermophilus*, *Cynomys*, *Tamias*, and *Tamiasciurus*. Further reduction in number because of loss of vertebrae distal to seventh. Transverse processes well developed back to vertebra with incisure; completely divided into cranial and caudal parts on succeeding vertebra; cranial and caudal parts minute or absent on other caudal vertebrae.

RIBS

Normally 12 ribs in Nearctic sciurids, rarely 13; all with costal cartilages. Seven true ribs in all forms except tree squirrels, which have eight. Five or four false ribs, two of which are floating. Neck decreases in length from first to tenth rib in correlation with decrease in length of transverse processes. Tuberculum absent on eleventh and twelfth ribs. First rib short and stout; succeeding ribs increase in length through sixth or seventh and decrease in length thereafter. Ribs consist of rounded cranial part and grooved caudal part. Angles indistinct.

Costal cartilages progressively longer and more sharply concave cranially from first through last true rib. First attaches to caudolateral surface of manubrium sterni, second between manubrium and first sternebra, next three (four in tree squirrels) between succeeding sternebrae, and last two cartilages of true ribs attach near caudal tip of last sternebra.

STERNUM

Body of manubrium irregularly pentagonal with slender caudal extension, jugular notch shallow, strong crest on ventral surface, cranial part concave dorsally. Clavicular notches occupy most of craniolateral surfaces. First costal pits on caudolateral surfaces. Second costal pits on ventral part of caudal end of manubrium; dorsal part of caudal end articulates with cranial end of first sternebra. Ventral crest weak in *Marmota*. In *Cynomys* a rounded process present at cranial end of manubrium below jugular notch, lateral angles acute, and body of manubrium diamond-shaped. Cranial surface gradually curved, jugular notch small, and lateral angles acute in *Tamias*. Body of manubrium triangular in *Sciurus* and *Tamiasciurus*, rounded process at apex, lateral angles rounded. Manubrium in *Glaucomyx* distinctive; crest absent, Y-shaped, wider than long, clavicular notches and first costal pits respectively on cranial and caudal surfaces of the two cranial branches near the tips.

Five sternebrae in body of sternum of *Sciurus*, *Tamiasciurus*, and in one representative each of subgenus *Citellus* and *Neotamias*; four or five sternebrae in *Marmota*;

² Methods of taking measurements for table 2. 1) Length of vertebral column: measured along midline of ventral surface; caudal vertebrae not included. 2) Length of sacral vertebrae: if four vertebrae are present, only the first three are included in the measurement. 3) Length of scapula: measured from highest point on medial rim of glenoid fossa to point on vertebral border in line with scapular spine. 4) Width of scapula: perpendicular distance between parallel lines through most cranial point on cranial border and most caudal point on axillary border. 5) Length of humerus: distance between proximal point of head and distal point of medial rim of trochlea. 6) Length of radius: greatest length. 7) Length of olecranon: distance between most distal point on proximal border of semilunar notch and proximal point of ulna. 8) Length of ox coxae: greatest length of dorsal part. 9) Length of femur: distance between most proximal point of greater trochanter and most distal point of femur. 10) Length of tibia: greatest length. 11) Length of sternum: greatest length along ventral surface; does not include xiphisternum.

four sternebrae in other animals examined. Last sternebra of *Neotamias* extends caudal to sixth costal pits farther than in other sciurids; seventh costal pits correspondingly not contiguous to sixth. Last sternebra in terrestrial squirrels and chipmunks may be composed of two fused sternebrae. This condition is intermediate to that in terrestrial squirrels, in which sixth and seventh costal pits are contiguous, and tree squirrels, in which they are at opposite ends of the fourth sternebra. Sternebrae decrease in length from first to last; flat dorsally and laterally and ridged ventrally. Bony part of xiphoid process slender and slightly flattened. Large xiphoid cartilage present.

The sternum, exclusive of xiphoid process, is relatively longer in *Otospermophilus*, *Ammospermophilus*, *Sciurus*, and *Tamiasciurus* than in other sciurids; relatively shorter in *Glaucomys* (see table 2).

Discussion.—The vertebral column of squirrels is a conservative part of the skeleton in comparison with the skull and appendicular parts. For this reason the length of the column, exclusive of the caudal vertebrae, is taken as the standard for computing the relative lengths of the sternum and relative sizes of the parts of the appendicular skeleton (see table 2).

Sciurids normally possess seven cervical, twelve thoracic, and seven lumbar vertebrae. There are three sacral vertebrae in tree and flying squirrels and chipmunks, four in marmots and prairie dogs, and three or four in ground squirrels. Three is probably the primitive number since *Palaearctomys montanus* had three and since this number appears to be stable in living representatives of the phyletic lines of tree squirrels, flying squirrels, and chipmunks which had diverged prior to the Upper Miocene. The presence of four sacral vertebrae is correlated with fossorial habits but is as yet not stabilized in the ground squirrels. The number of caudals varies from 15 to 26.

The relative lengths of the regions of the vertebral column, exclusive of the caudal region, are given in table 2. The cervical region is relatively longest in *Marmota* and is longer in *Otospermophilus*, *Ammospermophilus*, and *Cynomys* than in other sciurids. Externally the neck does not appear to be longer in these forms because it is stouter. The lumbar region is relatively longest in the subgenus *Citellus* and *Ictidomys* and is relatively shortest in *Glaucomys*. The three sacral vertebrae of tree squirrels, chipmunks, and flying squirrels are relatively longer than the corresponding three of other sciurids.

The supraspecific differences apparent in the vertebral column are, for the most part, adaptive and add little to our knowledge of the phylogeny of squirrels. A study of the column in a large number of specimens, combined with a detailed study of the activities of the animals, would make an excellent problem in functional anatomy. The processes of the vertebrae are, in general, longer in tree and flying squirrels than in chipmunks and terrestrial sciurids, in correlation with the probable greater mobility of the column. The extent of the pelvic articulation and the stoutness of the sacrum are in direct ratio to the fossorial tendencies of the several supraspecific groups. In the form of the pelvic articulation chipmunks resemble the terrestrial types more closely than the arboreal types.

Tree squirrels have eight true ribs and four false ribs. Other Nearctic sciurids have seven true and five false ribs.

The manubrium sterni of flying squirrels differs in form from that of other Nearctic sciurids. In other sciurids the general form is about the same, but the

manubrium of tree squirrels differs in minor details from that of terrestrial squirrels and chipmunks. The number of sternbrae is individually variable, but five are characteristic of tree squirrels and four are characteristic of other sciurids, except marmots, which have four or five sternbrae.

Appendicular Skeleton

PECTORAL GIRDLE AND APPENDAGE

Scapula.—Axillary border slightly convex; axillary ridge inclined caudolaterad. Vertebral border slants cranial and slightly ventrad from caudal angle; usually bends sharply at cranial angle to join cranial border, but cranial angle rounded and indistinct in some individuals. Subscapular fossa divided into three (rarely four) parts by two (rarely three) subscapular ridges. Caudal subscapular ridge located at base of axillary ridge; arises on medial surface of infraglenoid tuberosity and terminates below caudal angle. Cranial subscapular ridge arises on medial surface of neck and ends a short distance below dorsal part of cranial border. Coracoid joins head at right angle; highly variable in shape, convex cranially. Metacromion large; directed caudad. Acromion extends cranioventrad from metacromion; long and slender. Acromial tuberosity, for origin of acromiodeltoideus muscle, on ventral margin of acromion. Fossa for teres major muscle small and flattened; cranial edge formed by vertebral end of axillary border; caudal edge formed by low and short ridge running on subscapular surface from caudal angle. Vertebral border thickened, especially at end of scapular spine.

Cranial angle sharp-cornered in *Marmota* and *Cynomys*. Scapular notch relatively deeper in *Cynomys* than in other Nearctic sciurids, and metacromion relatively largest in *Marmota*.

Scapulae of chipmunks, tree squirrels, and flying squirrels differ from those of terrestrial squirrels in the following features: axillary ridge nearly perpendicular to surface of scapula, vertebral border inclined more nearly ventrad from caudal angle, vertebral border joins cranial border in gradual curve, and cranial angle indistinct, only the cranial subscapular ridge present, caudal edge of fossa for teres major prominent and fossa a definite groove. Infraspinous fossa deeper in chipmunks and tree squirrels than in other sciurids. In *Glaucomys* axillary border straight; axillary ridge lower and infraspinous fossa shallower than in other sciurids. Vertebral border inclined more nearly ventrad from caudal angle in *Sciurus* than in *Tamias* and *Tamiasciurus*; more inclined in *Glaucomys* than in *Sciurus*. Fossa for teres major long and shallow in *Glaucomys*, relatively shorter and deeper in *Neotamias*, and relatively largest and deepest in *Sciurus* and *Tamiasciurus*. In tree squirrels coracoid relatively longer; metacromion relatively smaller; acromial tuberosity located nearer tip of acromion; acromion relatively shorter, broader, and blunter. In *Glaucomys* base of coracoid more massive and coracoid relatively longer than in other squirrels; metacromion rounded and rudimentary; acromion reduced to short knob.

Scapula longer in comparison with length of vertebral column in *Otospermophilus*, *Ammospermophilus*, *Callospermophilus*, and *Neotamias*; intermediate in length in *Cynomys*, *Sciurus*, and *Tamiasciurus*; shorter in other sciurids, except *Marmota*; specifically variable in *Marmota* (see table 2). Scapula narrower in comparison with length in *Ammospermophilus*, *Callospermophilus*, *Neotamias*, and *Glaucomys* than in other squirrels.

The scapulae of ground squirrels, marmots and prairie dogs are similar and differ from those of tree and flying squirrels and chipmunks in many respects. Chipmunks differ from tree and flying squirrels and resemble the terrestrial squirrels in the shape of the metacromion, acromion, and coracoid. Tree squirrels differ from flying squirrels in the conformation of the axillary border and ridge, fossa for teres major, coracoid, metacromion, and acromion.

Clavicle.—Large in all sciurids. Elongated, slender, slightly sigmoid, spoon-shaped; compressed craniocaudally. Acromial end about twice as broad as sternal end. Coracoclavicular fossa in caudal surface of acromial end.

Acromial end relatively narrower and sternal end relatively larger in subgenus *Citellus* than in other ground squirrels. Shallow notch present on ventral margin of sternal end in *Ammospermophilus*. In *Cynomys* and *Marmota* coracoclavicular fossa broader and shallower than in other sciurids. In *Tamiasciurus* part around coracoclavicular fossa expanded and separated from acromial end by constricted area; acromial end smaller than in *Otospermophilus*. *Sciurus* lacks the constricted area but otherwise resembles *Tamiasciurus*. In *Glaucmys* clavicle relatively longer and slenderer than in other sciurids; coracoclavicular fossa reduced; sternal end nearly as large as acromial end.

Squirrels may be divided into three groups as regards the structure of the clavicle: terrestrial squirrels and chipmunks, tree squirrels, and flying squirrels.

Humerus.—Moderately stout; muscular processes large. Greater tubercle craniolateral to head, about two and one-half times as large as lesser tubercle; concavity in lateral surface for infraspinatus muscle. Lesser tubercle craniomedial to head; depression on medial surface for origin of subscapularis muscle. Deltoid ridge strong; on craniolateral surface; extends from greater tubercle caudad for about four-tenths length of humerus. Lateral epicondylar ridge high; extends laterocaudad from point on caudal surface of humerus opposite deltoid tuberosity to lateral epicondyle; groove present on caudal surface of distal end. Lateral epicondyle continuous with ridge but slightly broader; depressions on lateral and distal surfaces for attachments of extensor digitorum quinti and carpi ulnaris muscles. Medial epicondyle short and stout; much larger than lateral condyle; one caudal and two medial rugosities; excavated cranially, distally, and caudally. Medial epicondylar ridge short; extends laterodistad from craniodistal end of shaft to proximomedial margin of epicondyle. Entepicondylar foramen usually present. Condyles indistinctly separable into lateral capitulum and larger medial trochlea, the latter with sharply ridged medial margin. Well developed coronoid fossa on cranial surface of humerus proximal to condyles; smaller olecranon fossa in corresponding position on caudal surface; thin lamina separating the two fossae penetrated by supra-trochlear foramen in some individuals.

Entepicondylar foramen present in all specimens examined of *Ictidomys*, *Callospermophilus*, *Cynomys*, *Tamiasciurus*, and *Glaucmys*; absent in 4 specimens of *Citellus townsendii*, 11 of 12 *C. columbianus*, 1 of 4 *C. parryi*, 4 of 8 *C. tereticaudus*, 8. *C. mohavensis*, 1 of 10 *Ammospermophilus leucurus*, 1 of 4 *Marmota*, and 1 humerus of *Sciurus griseus*.

In *Marmota* and *Cynomys* deltoid ridge broader proximally than in *Otospermophilus*. In *Neotamias* lesser tubercle smaller and humerus slenderer; lateral epicondylar ridge begins distal to level of deltoid tuberosity. In *Tamiasciurus* and *Sciurus* head relatively smaller, deltoid ridge less inclined laterad and relatively shorter, and medial epicondyle longer and less robust than in terrestrial sciurids and chipmunks; proximal end of lateral epicondylar ridge distal to level of deltoid tuberosity as in *Neotamias*. Humerus of *Glaucmys* long and slender, general appearance smooth, deltoid and lateral epicondylar ridges low and short, ridge between entepicondylar foramen and coracoid fossa thin, medial epicondyle small, condyles relatively short and deep, trochlea with slightly raised medial margin.

Humerus relatively short in comparison with length of vertebral column in subgenus *Citellus*, *Ictidomys*, *Xerospermophilus*, *Cynomys*, and *Marmota*; intermediate in relative length in *Otospermophilus*, *Ammospermophilus*, *Callospermophilus*, *Neotamias*, *Sciurus*, and *Tamiasciurus*; relatively long in *Glaucmys*. In comparison with length of front leg, humerus longest and radius shortest in terrestrial sciurids, except *Ammospermophilus*; both intermediate in length in *Ammospermophilus*, *Neotamias*, and *Tamiasciurus*; humerus shorter and radius longer in *Sciurus*; humerus shortest and radius longest in *Glaucmys* (see table 2). Depth of humerus at deltoid tuberosity relatively greater in *Cynomys* and much smaller in *Glaucmys* than in other sciurids.

As regards humeri, chipmunks show greater resemblance to tree squirrels than to terrestrial forms. In flying squirrels the humerus is markedly different from that of other sciurids. A general correlation exists between the habits of

the animal and the length of the humerus. The more fossorial the squirrel the shorter the humerus in relation to the length of the body and the longer the humerus in comparison with the length of the front leg.

Radius and Ulna.—Head of radius articulates with radial notch of ulna; proximal articular surface continuous with distal surface of semilunar notch. Radius and ulna held together by ligaments extending between shafts from a point distal to tuberosity of ulna to distal epiphyseal lines. These ligaments tend to ossify in *Marmota* and to a lesser degree in *Cynomys*. Consequently, mobility is sacrificed for strength in these fossorial forms. A slight elevation on interosseus crest marks attachment of proximal ligament to ulna in terrestrial sciurids and chipmunks; elevation prominent in tree squirrels, and this part of shaft deeper than the ends. Length of line of contact between distal ends of radius and ulna greater in chipmunks and tree squirrels than in terrestrial squirrels. In flying squirrels distal halves of shafts fused.

The following gradients in features of the radius and ulna are discernible in passing from the more fossorial sciurids, through the less fossorial terrestrial species, chipmunks, and tree squirrels to flying squirrels: decreased stoutness, reduction in size of distal ends, increased length in comparison with length of vertebral column and in comparison with length of front leg, and decreased length of olecranon in comparison with length of ulna (see table 2).

Radius.—Slightly concave caudomedially; proximal end smaller than distal; shaft without strong ridges. Neck a subcylindrical constriction distal to head. Low and rounded tuberosity for insertion of biceps muscle on caudal surface of radius distal to neck. A small prominence on lateral surface, cranial to biceps tuberosity, for origin of abductor pollicis longus muscle. A low oblique ridge extends from lateral side of neck to middle of distal end of cranial surface. A low pronator ridge present on medial margin from biceps tuberosity to distal epiphysis; stronger near distal end. Blunt styloid process near medial side of irregular carpal articular surface; a rounded process medial to styloid process.

Abductor pollicis longus prominence larger in *Otospermophilus* than in other ground squirrels. Pronator and lateral oblique ridges sharper and caudal surface of radius more deeply grooved distally in *Ammospermophilus*. Distal end of pronator ridge elevated for shorter distance in subgenus *Citellus* than in other ground squirrels; fossa on disto-medial surface shorter.

Radius stout in *Marmota*, slightly less stout in ground squirrels and *Cynomys*, slender in *Neotamias*, *Sciurus*, and *Tamiasciurus*, and very slender in *Glaucomys*. Distal epiphysis larger than proximal end in terrestrial sciurids and chipmunks; ends about same size in tree and flying squirrels. Proximal articular surface more rounded in *Neotamias* and *Glaucomys* than in *Otospermophilus*; angular and slightly wider than long in tree squirrels. In *Marmota* a small fossa usually occurs at the site of the abductor pollicis longus prominence; prominence strong in *Cynomys*. A low ridge joins the margin of proximal articular surface and abductor pollicis longus prominence in tree and flying squirrels. Distal end of shaft relatively heavier in terrestrial squirrels and chipmunks than in other sciurids; this is weakest part of shaft in *Glaucomys*.

In comparison with the length of the vertebral column, the radius is short in the subgenus *Citellus*, *Ictidomys*, *Xerospermophilus*, *Cynomys*, and *Marmota*; intermediate in *Otospermophilus* and *Callospermophilus*; longer in *Ammospermophilus*, *Neotamias*, *Sciurus*, and *Tamiasciurus*; and longest in *Glaucomys* (table 2).

Ulna.—Semilunar notch in cranial surface of ulna near proximal end; proximal edge of notch more nearly vertical than distal edge and with tricipital process on lateral margin; coronoid process on distal edge, medial to smaller radial notch; articulates with trochlea of humerus. Olecranon 15.0% to 16.1% of ulnar length; lateral surface

occupied by shallow tricipital fossa; cranial edge and medial anconeal fossa concave; caudal margin perpendicular to proximal margin; weakly developed tricipital ridge on caudal surface for insertion of triceps lateralis muscle; small anconeal process on proximal margin of anconeal fossa separated by notch from small process on proximo-caudal angle. Shaft gradually diminishes in size from proximal to distal end. Rounded caudal border of shaft extends from tricipital ridge to distal epiphysis. Small ulnar tuberosity, for insertion of brachialis muscle, located distal to coronoid process. Deep lateral fossa in lateral surface of shaft. Pronator ridge extends proximad on medial surface from distal epiphyseal line; continuous with indistinct medial border, which extends from pronator ridge to ulnar tuberosity; pronator fossa and cranial fossa located between interosseus crest and pronator ridge and medial border respectively; pronator fossa much shorter but more clearly delimited than cranial fossa. Head roughened laterally and concave medially; blunt styloid process at tip.

Proximal end of olecranon turned more nearly mediad in *Ammospermophilus*. Lateral fossa smaller in *Ictidomys* and larger in *Otospermophilus* than in other ground squirrels. Medial fossa smaller or absent in marmots, prairie dogs, and ground squirrels other than *Ammospermophilus* and *Callospermophilus*, and interosseus crest correspondingly thicker. Tricipital ridge more prominent in *Marmota* and *Cynomys*; olecranon relatively longer in the former.

In *Neotamias* lateral fossa long and deep; shaft slenderer and distal end more reduced than in *Otospermophilus*. In *Sciurus* and *Tamiasciurus* tricipital ridge stronger; process on proximocaudal angle of anconeal fossa smaller and tricipital process larger; tuberosity indistinct; lateral fossa deeper; medial border absent and a well developed fossa occupies cranial and medial surfaces, shaft consequently narrower and interosseus crest thinner and sharper; pronator ridge and fossa rudimentary; middle of shaft deeper than either end; distal end relatively smaller than in *Neotamias*.

In *Glaucomys* olecranon relatively much shorter than in other sciurids; tricipital ridge strong; tuberosity minute; shaft reduced to a filament of bone, deep lateral fossa consequently reduced in length, and medial border, pronator ridge, and pronator fossa are absent; distal end reduced to styloid process and two minute rugosities.

Certain trends in characters are worthy of mention. The olecranon is in line with the shaft in ground squirrels, marmots, and prairie dogs; is slightly inclined craniad in chipmunks; is more inclined in tree squirrels; and reaches its maximum inclination in flying squirrels. In the same sequence the lateral and cranial fossae are deeper, the shaft is narrower and relatively weaker, and the distal end is more reduced. An exception occurs in the development of the fossae in flying squirrels, in which they are necessarily small because of the reduced size of the distal part of the shaft.

In length, the ulna in comparison with the vertebral column follows the same trend as the radius (see page 298).

Carpus.—When the muscles of the arm relaxed, the proximal end of the ulna is caudal to the radius and, since the radius curves mediad toward its distal end, the distal end of the ulna is caudolateral to this end of the radius. The hand is consequently turned mediad at an angle of about 25° to the vertical plane. Supination to slightly more than 90° is possible. In marmots, except young animals, the carpus is kept in a prone position at all times; and in flying squirrels pronation and supination are limited. Pronation to slightly more than the horizontal is possible in other squirrels, although the movements are more restricted in *Cynomys*, less restricted in ground squirrels and *Neotamias*, and least restricted in *Sciurus* and *Tamiasciurus*.

Os scapholunaris.—Largest carpal; represents fused navicular and lunate bones.

Rounded proximally for articulation with radius; distal surface nearly vertical and slightly concave with centrale occupying center of concavity. Articulates with triquetrum laterally and with major and minor multangulars distally. Caudomedial margin prolonged into a process between major multangular, first metacarpal, and falciform. Rounded craniolaterally, for articulation with falciform, and slightly concave ventrally.

Os triquetrum.—Irregularly rectangular in cranial view. Shaped like digital pad and toe of cat, the "pad" medial and "claw" distal to upper end of pisiform; claw touches base of fifth metacarpal when hand is flexed. Articulates distally with hamate and medially with scapholunar. A small notch on proximolateral margin for styloid process of ulna. Relatively larger and notch for styloid process located more proximally in *Cynomys*.

Os pisiforme.—Extends caudad from styloid process of ulna. Distal end larger than proximal. Smaller in *Amnospermophilus* and *Xerospermophilus* than in other sciurids.

Os falciforme.—Convexly clavate in medial view with notch in proximal end for articulation with first metacarpal; extends caudomedial and slightly distad. Forms medial surface of a deep notch on palmar surface of wrist; pisiform forms lateral border of notch and other carpal bones form roof. Space between distal tips of falciform and pisiform closed by ligaments. Articulates cranioproximally with scapholunar. Most variable of carpal bones. Short and blunt in *Sciurus* and *Tamiasciurus*, greatly reduced in *Glaucomys*, large and triangular in *Cynomys*, long and pointed in subgenus *Citellus* and in *Otospermophilus*, of moderate length and pointed in other forms.

Os multangulum majus.—Proximal apex between minor multangular and medial process of scapholunar; rounded medial apex articulates with notch in head of first metacarpal; distal apex articulates with medial side of head of second metacarpal.

Os multangulum minus.—Convex distal surface fits into notch in head of second metacarpal. Articulates proximally with centrale and scapholunar and medially with major multangular.

Os centrale.—Proximal surface in contact with scapholunar, lateral surface with capitate, and distal surface with major multangular and lateral process of head of second metacarpal.

Os capitatum.—Concave medially for reception of centrale and concave laterally for articulation with medial surface of hamate. Rounded distal surface fits into notch in head of third metacarpal and touches lateral surface of head of second metacarpal. Proximal point located between centrale, hamate, and scapholunar. In *Sciurus*, *Tamiasciurus*, and *Glaucomys* capitate does not touch second metacarpal.

Os hamatum.—Proximal process passes distal to triquetrum and touches scapholunar. Articulates medially with capitate and third metacarpal and distally with heads of fourth and fifth metacarpals.

Metacarpus.—The length of the metacarpals from shortest to longest is 1-5-2-4-3 in terrestrial squirrels, 1-5-2-(3-4) in chipmunks, 1-5-2-3-4 in tree squirrels, and 1-2-5-(3-4) in flying squirrels. Metacarpals stout in *Cynomys* and *Marmota*; moderately stout in ground squirrels; slender in *Neotamias*; very long and slender in *Sciurus*, *Tamiasciurus*, and *Glaucomys*. First metacarpal short and broad; head with two rounded tuberosities; proximal end larger than distal. Second metacarpal about four times as long as first; head concave for reception of minor multangular. Shafts of second through fifth metacarpals narrower than ends, flattened; distal end of each with rounded process for articulation with first phalanx. Head of third metacarpal pointed in middle and with flattened medial and lateral surfaces for articulation with capitate and hamate bones. Head of fourth metacarpal convex. Head of fifth metacarpal with medial fossa for hamate bone and strong proximolateral process for muscle attachment.

Phalanges.—Pollex greatly reduced in all sciurids but relatively longest in *Neotamias* and *Cynomys*. It bears a flat nail in all forms except *Cynomys*, in which it bears a claw. Pollex has two phalanges and other digits have three. Proximal phalanges shorter than corresponding metacarpals, except on pollex, and of same relative length as metacarpals. Proximal phalanx of pollex short; concave on palmar surface; a small tuberosity on

each side of proximal and distal ends. Proximal phalanges of second through fifth digits each with two sesamoid bones on palmar surface of proximal end; sesamoids separated by grooves from two smaller tuberosities on phalanx, the four looking from palmar view like the bottom of a deer's foot; proximal ends concave for articulation with ends of metacarpals; margins of shaft turned downward; a minute elevation on either side near distal end; distal end spool-shaped. Intermediate phalanges of second through fifth digits concave proximally; shafts shorter than those of proximal series but similarly shaped. Ungual phalanx of pollex minute; a rounded tip surmounted by flat plate of bone under the nail. Ungual phalanges of other digits concave proximally and with a small process in middle of upper surface; rounded prominence on palmar surface above digital pad; distal part compressed and sharp-pointed, convex above and concave below, shaped like claw but shorter and blunter.

PELVIC GIRDLE AND APPENDAGE

Pelvic Girdle.—Basin broad and moderately deep; shallower in *Ictidomys*; narrow and deep in *Sciurus* and *Tamiasciurus*. Solid sacroiliac joint limited to middle part of medial surface of ilium (see below). Girdle stouter in *Marmota*. Girdle longer in comparison with length of vertebral column in *Otospermophilus*, *Ammospermophilus*, *Callospermophilus*, *Marmota*, *Neotamias*, *Sciurus*, *Tamiasciurus*, and *Glaucomys* (see table 2).

Os coxae.—Acetabulum located near dorsal surface about two-thirds of distance from cranial to caudal end; deep, circular, opens caudoventrally at acetabular notch. Pubis excluded from acetabulum by triangular acetabular bone. Cranial third of acetabulum formed by ilium and caudal half by ischium. Complete fusion of bones occurs early in life.

Ilium about twice as long as ischium; extends craniad to level of articulation of sixth and seventh lumbar vertebrae. Body triangular in cross section; apex of triangle pointed laterally. Cranial part of shallow greater sciatic notch on dorsal border. Anterior inferior spine large and rounded; separated from cranial lip of acetabulum by shallow groove. Iliopectineal ridge small. Small iliopectineal eminence separated from pectineal process of pubis by shallow notch. Wing of ilium curves cranio-laterad from sacroiliac joint; depth much greater than width; dorsal and ventral borders nearly parallel; medial surface concave in vertical axis and convex longitudinally; lateral surface divided by iliac ridge into slightly excavated superior and smaller inferior gluteal fossae; surfaces of fossae meet at right angle; inferior gluteal fossa longitudinally grooved, a ridge usually present instead of a groove in subgenus *Citellus* and occasionally present in other ground squirrels; iliac crest low and weakly recurved; anterior superior spine small and rounded. In *Cynomys* wings more divergent and massive, iliac crest stouter, anterior superior spine extends lateroventrad as a longer process, and longitudinal ridge in inferior gluteal fossa well developed. In *Marmota* wings as broad as deep, equilaterally triangular in transverse section, stout; inferior gluteal fossa almost as large as superior and with strong longitudinal ridge, iliac crest well developed but not recurved, anterior superior spine larger, and superior gluteal fossa less concave cranially. Iliac wings of *Tamias*, *Sciurus*, *Tamiasciurus*, and *Glaucomys* markedly different from those of terrestrial sciurids: articulation with sacrum shorter, wings extend craniad beyond level of articulation of sixth and seventh lumbar vertebrae and are greatly compressed, cranial end flattened (triangular in terrestrial forms), iliac crest limited to cranial tip and not recurved, anterior superior spine minute in chipmunks and absent in tree and flying squirrels, iliac ridge broader and gluteal fossae correspondingly reduced in size, dorsal and ventral borders curved laterad and gluteal fossae correspondingly deepened, and angle of junction of gluteal fossae at iliac ridge about 120°. Wings in *Glaucomys* relatively slenderer than in other sciurids.

Ischium heavier than pubis, much weaker than ilium. Concavity on medial surface of body continuous with depression in medial surface of caudal end of body of ilium; ridges on dorsal and ventral margins of concavity more prominent in tree and flying squirrels. Acetabular notch in cranio-lateral margin. Dorsal surface slightly concave, wider cranially than caudally. Greater and lesser sciatic notches confluent, their junction

marked by small ischial spine on medial side of dorsal border. Dorsal ramus heavier in terrestrial squirrels than in other sciurids. Ischial tuberosity large. Lateral processes small; absent in *Cynomys*. Ventral ramus compressed; medial surface flattened and lateral surface slightly concave; cranial part of lateral surface separated by low ridge from roughened caudal part in *Tamias*, *Sciurus*, and *Tamiasciurus*; joins pubis at caudal end of pubic symphysis and may enter slightly into symphysis. In *Tamias*, *Sciurus*, *Tamiasciurus*, and *Glaucomys* ventral part of ventral ramus turned more sharply cranio-ventrad, a deeper notch present between ventral rami caudal to symphysis, and ventral ischial tuberosity larger. Ventral ischial tuberosity varies in size with age and sex; larger in males.

Iliopectineal region of pubis deeper and pectineal spine larger in tree squirrels than in other squirrels. In correlation with this cranial border of pubis more convex, cranial ramus extends more nearly ventrad from acetabulum, and distance from cranial end of pubic symphysis to ventral ischial tuberosity relatively longer. Symphysis moderately long in terrestrial squirrels, short in *Tamias*, and very short in *Glaucomys*. In the latter its length is less than its width.

The parts of the pelvic girdle which exhibit significant supraspecific differences are: iliac wings, ventral ramus of ischium, and pubis. On the basis of these differences the Nearctic sciurids are clearly divisible into two groups: (1) terrestrial squirrels, and (2) chipmunks, tree squirrels, and flying squirrels. *Cynomys* and *Marmota* differ from the ground squirrels in the form of the iliac wings. The tree squirrels differ from chipmunks and flying squirrels in the structure of the cranial ramus and symphysis of the pubis. The symphyseal regions of chipmunks and flying squirrels are distinctive.

Femur.—Articular part of head hemispherical; fossa for ligamentum teres minute. Neck constricted, oval in cross section; joins shaft at angle of about 135° . Greater trochanter smaller than head, from which it is separated by shallow notch; shorter in subgenus *Citellus*. Deep trochanteric fossa restricted to medial surface of greater trochanter. Lesser trochanter extends caudoproximomedial in terrestrial squirrels and medial in chipmunks and tree and flying squirrels; much smaller than greater trochanter. Lesser trochanter short and conical in subgenus *Citellus*, *Ictidomys*, *Cynomys*, and *Marmota*; relatively longer and usually pointed in other ground squirrels and in *Tamias* and *Glaucomys*; and most prominent in tree squirrels, in which it extends medial as far as does the head. Low trochanteric ridge present in small species and absent in large species; correlated with size of animal. Third trochanter a small but definite process that is relatively larger in large individuals; situated slightly more distally than lesser trochanter, except in *Marmota* and *Tamias*. Lateral ridge prominent and flattened in tree squirrels and rudimentary in flying squirrels; intermediate in size in other forms.

Shaft narrowest at point caudal to third trochanter and becomes gradually broader from this point to distal end; markedly convex cranially and slightly convex caudally; indistinct ridges on lateral and medial borders. Proximal end of femur flatter than shaft. Distal end of femur enlarged and bent caudad at epiphyseal line; less enlarged in *Glaucomys* than in other sciurids.

Distal epiphysis completely fused with shaft only in old individuals. Shallow patellar groove extends proximad past epiphyseal line; limited medially and laterally by sharp ridges; broader in tree and flying squirrels. Intercondylar notch deep and rugose; limited proximally and distally by well-developed ridges. Medial and lateral sesamoid bones present proximal to medial and lateral margins of corresponding condyles. Medial epicondyle larger than lateral, neither with well marked processes; lateral epicondyle more rugose. Fossa on medial epicondyle for attachment of tibial collateral ligament distinct. Medial condyle extends caudad farther than lateral; broader than lateral in subgenus *Citellus*, *Ictidomys*, *Cynomys*, and *Marmota* and about same size in other sciurids.

Femur slender in *Glaucomys* and slightly less so in *Sciurus* and *Tamiasciurus*. In ground squirrels, least robust in *Ammospermophilus* and *Callospermophilus*; stouter in

Xerospermophilus, *Ictidomys*, and *Otospermophilus*; in subgenus *Citellus* varies from stoutness of *Ictidomys* in small species to very stout in large species. Femur in *Cynomys* as in large species of subgenus *Citellus*; in *Marmota* as in *Otospermophilus*; in *Tamias* as in *Ammospermophilus*.

The lengths of the femur, tibia, and hind leg in comparison with the length of the vertebral column are shortest in the subgenus *Citellus*, *Ictidomys*, *Xerospermophilus*, *Cynomys*, and *Marmota*; longer in *Otospermophilus* and *Callospermophilus*; still longer in *Ammospermophilus*, *Tamias*, *Sciurus*, and *Tamiasciurus*; and longest in *Glaucomys*. The femur is longer in comparison with the length of the hind leg in terrestrial squirrels, except *Ammospermophilus*, than in chipmunks and tree and flying squirrels. Thus, in arboreal forms the bones of the hind leg are longer in comparison with the length of the body, and the tibia is longer and the femur is shorter in comparison with the length of the hind leg (see table 2).

Tibia.—Distal part of fibula, except epiphysis, fused to caudolateral surface of distal part of tibia. Length of fused area least in *Cynomys* (about 12% of length of tibia), slightly greater in ground squirrels and *Marmota*, and successively greater in *Sciurus* and *Tamiasciurus* (about 20%), *Neotamias* (about 25%), and *Glaucomys* (about 37%). Relative massiveness of tibia and fibula same as for femur (see page 302).

Lateral condyle larger than medial; usually extends farther caudad. Intercondylar fossa shallow and rugose. Process on caudolateral margin of lateral condyle, for articulation with head of fibula, relatively larger in terrestrial squirrels than in other sciurids. Proximal half of tibia roughly triangular in transverse section; angles formed by cranial, medial, and interosseus borders; bent caudad so that it is convex cranially and concave caudally. Proximal end more enlarged and curvature greater in terrestrial sciurids. Among ground squirrels, curvature of proximal and greatest in subgenus *Citellus*. Tibial tuberosity and proximal part of cranial border strongly developed in ground squirrels, prairie dogs and marmots, of medium size in chipmunks and tree squirrels, and weak in flying squirrels. Rugosity on cranial border, for insertion of semitendinosus, more prominent in *Otospermophilus* and *Ammospermophilus* than in other ground squirrels. All of these features correlated with development of extensor muscles of leg, which are most powerful in fossorial and heavy-bodied forms.

Lateral fossa shallow in terrestrial squirrels and chipmunks; deeper and longer in tree and flying squirrels; flatter in *Otospermophilus* and *Callospermophilus* than in other ground squirrels. Popliteal fossa deep in terrestrial squirrels and chipmunks as result of elevation of lateral and medial crests of fossa and greater caudal curvature of proximal end of tibia; smaller and shallower in tree squirrels; nearly flat in flying squirrels. Popliteal line indistinct and fossa not clearly delimited distally. Small process on medial border for attachment of flexor digitoris longus.

Distal end of tibia stouter and more angular in terrestrial than in other sciurids. Process at junction with fibula shorter and more prominent in terrestrial forms, lower and longer in tree squirrels and chipmunks, and indistinct in flying squirrels. Lateral articular surface of distal epiphysis larger and less concave than medial articular surface. Cranial part of crest dividing articular surface bends medially to join base of cranio-medial process and is elevated to form a tubercle in depression between cranio-medial and cranio-lateral processes. Medial malleolus longer in tree squirrels than in terrestrial forms and chipmunks; all distal processes short in flying squirrels.

The length of the tibia in comparison with the lengths of the body and hind leg is discussed above.

Fibula.—Slender and nearly straight in all sciurids. Relatively stouter in *Marmota*, *Cynomys*, and subgenus *Citellus*; of medium stoutness in *Otospermophilus*; weak in other squirrels. Head clavate; curves proximolaterad and ends in small peroneal process; oval surface proximomedially for articulation with proximal end of tibia; rounded protuber-

ance on caudal surface for attachment of soleus muscle. Proximal part of shaft flattened, its medial surface occupied by flexor fibularis fossa. This fossa shallow in terrestrial forms, except *Ammospermophilus*; deep and narrow in *Ammospermophilus*, chipmunks, and tree squirrels, in which lateral and medial margins of fossa are sharp ridges; a minute groove in *Glaucomys*. Distal third of shaft concave medially. Part fused with distal end of tibia not as prominent as corresponding part of tibia; located on medial surface proximal to articular facet for talus. Distal epiphysis compressed; terminates in two rounded processes, of which the cranial lateral malleolus is larger than the caudal process. Lateral malleolus articulates with lateral surface of trochlea of talus; caudal process ends freely.

Tarsus.—Nine tarsal bones arranged in three rows; talus, calcaneum, and medial tarsal in proximal row; navicular and medial sesamoid in intermediate row; first, second, and third cuneiforms and cuboid in distal row.

Talus.—Body longer laterally than medially; lateral length about equal to width of talus. Trochlea pulley-like; articulates cranially with distal end of tibia and is only supporting element for leg; lateral articular surface comma-shaped, attached to distomedial surface of lateral malleolus of fibula by ligament; medial surface also comma-shaped but with pointed end directed distad, articulates with medial malleolus of tibia; lateral half of caudal surface concave for articulation with calcaneum; groove of talus deep. Neck extends distomedial from medial half of distal part of body; short and stout; shallow groove to receive cranial end of ridge on distal surface of tibia present at junction with body; medial two-thirds of caudal surface occupied by facet for articulation with calcaneum. Head little wider than neck; distal surface transversely oval; articulates with medial tarsal and navicular. Talus more massive in *Cynomys* and *Marmota*. Talus of *Tamias*, *Sciurus*, and *Tamiasciurus* differs from that of *Otospermophilus* as follows: body shallower, medial length of body less in comparison with lateral length, groove of talus shallow, groove on proximocranial surface of neck deeper, neck longer and directed more nearly medial, medial part of head more expanded. Talus of *Glaucomys* similar to that of *Sciurus* but groove on neck shallow and head little longer than neck.

Calcaneus.—Cruciform; transverse part slants craniomedial. Proximal surface with large groove for tendo calcaneus. Proximal process (heel) massive; width slightly less than depth in terrestrial squirrels, but process compressed in chipmunks and tree and flying squirrels. Large facet near middle of cranial surface for articulation with body of talus; another facet on cranial surface of sustentaculum tali for articulation with neck of talus; the former facet longer and less convex in terrestrial squirrels than in other forms. Distomedial surface of sustentaculum tali touches medial tarsal bone. Peroneal process bears a minute groove laterally and a large, shallow groove caudally. Sustentaculum tali on same level as peroneal process in terrestrial sciurids but located more distally in chipmunks and tree and flying squirrels. Facet for articulation with cuboid slightly concave. Ridge on caudal surface, lateral and distal to sustentaculum tali, stronger and groove on caudal surface of sustentaculum deeper in terrestrial sciurids than in other forms.

Os tarsale mediale.—Roughly hemispherical in terrestrial forms but flattened in chipmunks and tree and flying squirrels. In the latter two groups a minute process present on proximal surface for articulation with sustentaculum tali. Articulates medially with head of talus, distally with first cuneiform, and laterally with medial sesmoid.

Os naviculare pedis.—Much wider cranially than caudally. Plantar process cylindrical in terrestrial squirrels and chipmunks; shorter and wider in tree and flying squirrels. Proximal surface occupied by large, concave facet for head of talus. Rounded tuberosity on medial surface articulates with first cuneiform and medial tarsal bones; sharply pointed in tree squirrels. Articulates distally with second and third cuneiforms and laterally with cuboid. A groove present below tuberosity for tendon of tibialis posterior muscle.

Os cuboideum.—Width greater than length in *Cynomys* and *Marmota*. Convex proximal surface articulates with calcaneum; larger than concave caudal surface, which articulates with fourth metatarsal and proximomedial tip of fifth. Articulates medially

with navicular and third cuneiform; a small canal present between distal portion and third cuneiform. Deep groove on plantar surface of distal part for tendon of peroneus longus muscle; ridge forming proximal margin of groove higher in terrestrial squirrels.

Medial sesamoid.—A minute, elongate bone extending caudad from its cranial attachment between medial tarsal and first cuneiform; may be attached only to first cuneiform.

First cuneiform.—Slightly convex laterally and concave medially; triangular in medial view with apex directed proximad. Process at proximal end extends caudolaterad. Lateral surface articulates with navicular, and tip with medial sesamoid. Distal surface concave vertically for articulation with head of first metatarsal. Articulates medially with second cuneiform and second metatarsal. Small process on plantar tip articulates with lateral process of head of first metatarsal.

Second cuneiform.—Concave on all surfaces. Fits into concavity in head of second metatarsal.

Third cuneiform.—Slightly deeper than wide. Flattened proximal and distal ends articulate respectively with navicular and third metatarsal. A pointed process extends from distomedial margin lateral to head of second metatarsal. Upper part of medial surface concave for articulation with second metatarsal and second cuneiform; rugose below.

Metatarsus.—Five well developed metatarsals. Metatarsals depressed and slightly concave caudally. Distal ends round for articulation with phalanges; two prominent tuberosities on plantar surface of distal ends for muscle attachment, thus resembling metacarpals. Proximal surface of first metatarsal convex; a prominent process extends laterad and articulates with head of second metatarsal. Lateral margin of concavity in head of second metatarsal larger and more rounded than medial margin. Proximal surfaces of third and fourth metatarsals flattened. Head of fifth metatarsal flattened on upper surface; a large process extends laterad from proximal end. First metatarsal much shorter than fifth but extends almost as far distad. In subgenus *Citellus*, *Ictidomys*, and *Cynomys* second and fourth metatarsals subequal, variable as to which is longer; fourth longer than second in *Otospermophilus*, *Ammospermophilus*, and *Callospermophilus*; and second longer than fourth in *Xerospermophilus*. In *Tamias*, *Sciurus* and *Tamiasciurus* second and fifth metatarsals subequal, first shorter, and fourth and longest metatarsal slightly longer than third. Metatarsals progressively longer from first through fifth in *Glaucomys*; fifth extends distad as far as third and slightly less distad than fourth. Lateral process from head of fifth metatarsal shorter and stouter in *Cynomys* than in other sciurids.

Metatarsus shorter and stouter in terrestrial squirrels than in chipmunks and tree and flying squirrels. In the former, metatarsus shorter in subgenus *Citellus* and in *Cynomys*; intermediate in *Otospermophilus* and *Callospermophilus*; slender in other ground squirrels. Metatarsus in tree squirrels long and slender, as in chipmunks, but slightly stouter. Metatarsus in *Glaucomys* longer, narrower, and weaker than in other sciurids.

Phalanges.—Number in first through fifth digits: 2-3-3-3-3. Similar in structure to those of hand but longer. Short and stout in subgenus *Citellus* and in *Cynomys*; progressively longer and slenderer in other ground squirrels, tree squirrels, chipmunks, and flying squirrels.

Discussion.—A comparison of the bones of the appendicular skeletons of Nearctic squirrels shows that most of these animals fall into three clearly defined groups with little overlapping in variable features. These groups are terrestrial, tree, and flying squirrels. A fourth group, the chipmunks, resembles terrestrial squirrels, particularly *Ammospermophilus*, in some variable features

but more closely resembles the tree squirrels. Most of the differences apparent in the appendicular skeletons are correlated with the habits of the several kinds of animals, and trends in the proportions of the parts of the appendicular skeleton are traceable from the more fossorial forms, through the less fossorial forms, chipmunks, and tree squirrels to flying squirrels. The following trends may be mentioned: increasing length of the limbs in comparison with the length of the vertebral column, decreasing length of proximal segments and increasing length of forearm and leg in comparison with the length of the limbs, increasing slenderness of bones of the limbs, decreasing size of the distal ends of the bones of the distal segments of the limbs, and decreasing length of the olecranon in comparison with the length of the ulna.

Baculum

Specimens examined: *Citellus (Otospermophilus) variegatus*, 10; *Citellus (Otospermophilus) beecheyi*, 2; *Citellus (Citellus) beldingi*, 2; *Citellus (Ictidomys) spilosoma*, 1; *Citellus (Ictidomys) tridecemlineatus*, 2; *Citellus (Ictidomys) mexicanus*, 2; *Citellus (Xerospermophilus) tereticaudus*, 8; *Citellus (Callospermophilus) madrensis*, 3; *Citellus (Poliocitellus) franklinii*, 1; *Ammospermophilus harrisi*, 5; *Cynomys mexicanus*, 3; *Cynomys gunnisoni*, 1; *Tamias (Neotamias) dorsalis*, 3; *Sciurus truei*, 9; *Sciurus aberti*, 2; *Glaucomys volans*, 1.

Proximal end of baculum in *Otospermophilus* enlarged into a knob, which is about twice as wide as shaft; proximal part of knob hollow. Shaft slender; proximal part bends slightly dextrally, and distal part curves slightly sinistrally and ventrally. Spoon-shaped ventral part of distal end of baculum joins shaft without abrupt change of direction; lateral margins bend nearly ventrad, and cavity of spoon consequently narrow and deep; from two to six spines present on each lateral margin; terminal spines of each side separated from each other by notch. A knob is present at distal end of dorsal surface of spoon.

Bacula of other ground squirrels and prairie dogs of same general type as that of *Otospermophilus*. Baculum in *Callospermophilus* smaller and relatively stouter; spoon relatively broader and shallower, joining shaft at angle of about 135° and bearing spines continuously around sides and distal margin. In subgenus *Citellus* spoon is wider and deeper than in *Callospermophilus* and rows of spines on margins are more divergent; otherwise as in *Otospermophilus*. In *Poliocitellus* spoon relatively larger than in subgenus *Citellus*; otherwise similar. Baculum of *Xerospermophilus* differs from that of subgenus *Citellus* in that it is relatively stouter and the spoon is relatively larger. The baculum of *Ammospermophilus* differs markedly from that of other ground squirrels; proximal end greatly enlarged and with a process on left side; spoon larger than remainder of baculum; spoon joins shaft at 90° angle, is wider than long, and small spines are continuous along its semicircular margin. In *C. (Ictidomys) spilosoma* the proximal end of baculum and shaft are as in *Callospermophilus*; spoon flatter than in other ground squirrels, is widely expanded, and joins shaft at angle of 135° ; processes arise from proximal surface of spoon on each side of shaft. Shaft in *C. (Ictidomys) mexicanus* and *C. (Ictidomys) tridecemlineatus* heavy and nearly straight; large notch in distal end of spoon through which dorsal knob is visible from a ventral view; lateral margins of spoon not curved as in other ground squirrels; rows of spines on margins of spoon converge distally at a right angle. Baculum of *Cynomys* resembles that of *Xerospermophilus*; but spoon is relatively larger and is swollen on left side at junction with shaft, and a process is present in corresponding position on right side.

Bacula of chipmunks, tree squirrels, and flying squirrels are of different types, but differ from those of terrestrial sciurids in the following features: proximal end not bulbous, shaft nearly straight, and spines and dorsal knob absent at distal end. Distal end slightly enlarged in chipmunks and flying squirrels and asymmetrical in flying squirrels and tree squirrels. In *Neotamias* distal end joins shaft at an angle of about

135°; a longitudinal blade-like ridge is present in middle of ventral surface of distal end. Baculum in *Sciurus* much larger than in other Nearctic squirrels; distal end blade-like; blade turned to left of shaft and twisted slightly out of plane of shaft; process present on right side of blade; shape of blade variable in different species. Baculum long and slender in *Glaucomys*; shaft twisted; deep longitudinal groove on dorsal and right sides of shaft passes ventral to overhanging ledge situated on dorsal side of distal end.

Discussion.—There is a type of baculum characteristic of each of the following groups: terrestrial squirrels, chipmunks, tree squirrels, and flying squirrels. Among the supraspecific groups of terrestrial squirrels, the baculum of *Ammospermophilus* has a markedly different configuration. The bacula of two of the species of *Ictidomys*, *C. mexicanus* and *C. tridecemlineatus*, are similar and have a distinctive form; but the third species of *Ictidomys*, *C. pilosoma*, has a baculum of a different shape. Either *C. pilosoma* is not as closely related to *C. mexicanus* and *C. tridecemlineatus* as has been assumed, or the form of the baculum is not of supraspecific significance in all groups of squirrels.

Muscular System

The order of arrangement of the major groups of muscles here followed is the phylogenetic one proposed by A. B. Howell (1936). The more detailed separation of the muscles into minor groups is based on common innervation and comparative myology and follows Hill (1937) except in a few minor points. The study of the muscles of rodents has now reached the stage where no doubt exists about the homologies of most muscles. Consequently, I have accepted the conclusions agreed upon by previous workers in the field, and have accurately determined the innervations only of the highly specialized superficial facial musculature. The terminology of Hill (1937) is followed almost in its entirety. The list of synonyms included in the discussion of each muscle will enable future students of the muscles of sciurids to use the literature without undue loss of time.

The following animals were dissected: *Citellus* (*Citellus*) *beldingi*, 3; *Citellus* (*Ictidomys*) *mexicanus*, 3; *Citellus* (*Poliocitellus*) *franklinii*, 2; *Citellus* (*Xerospermophilus*) *tereticaudus*, 3; *Citellus* (*Otospermophilus*) *variegatus*, 4; *Citellus* (*Otospermophilus*) *beecheyi*, 2; *Citellus* (*Callospermophilus*) *lateralis*, 3; *Ammospermophilus* *harisii*, 1; *Ammospermophilus* *interpres*, 3; *Tamias* (*Neotamias*) *speciosa*, 3; *Marmota* *flaviventer*, 2; *Cynomys* *gunnisoni*, 3; *Sciurus* *griseus*, 1; *Sciurus* *niger*, 1; *Tamiasciurus* *douglasii*, 1; *Glaucomys* *volans*, 1; *Glaucomys* *sabrinus*, 1. Most of these specimens were embalmed with a mixture of formalin (5%), carbolie acid (5%), glycerine (5%), and water (85%). The others were preserved in 8% formaldehyde. Upon reaching the laboratory all of the specimens were placed in a solution consisting of equal parts of glycerine, 95% alcohol, and water. The embalmed specimens were in excellent condition for dissection. Those originally preserved in formaldehyde were less satisfactory.

The usual method of study was to dissect muscle by muscle two specimens each of *Citellus* *variegatus* and *Citellus* *beecheyi* to determine the condition of each muscle in the subgenus *Otospermophilus*. Two additional specimens of *C. variegatus* were used to check doubtful points. The muscles of one representative of each of the other subgenera of *Citellus* and of each of the other genera of Nearctic sciurids were then compared with the muscles in *Otospermophilus*. If significant differences were apparent dissections of additional specimens were made. Differences in muscles are recorded only when they are judged to be indicative of more than age-variation, degree of contraction, or the habits of the individual dissected. The relative sizes of the processes where muscles attach to bones are used as supporting evidence of the relative strengths of the muscles.

In the following discussion *Otospermophilus* is used as the standard for the description of each muscle, except in the constrictor colli group, and the muscles of other squirrels are compared with this standard. In the constrictor colli group, *Sciurus* is selected as the standard because the primitive arrangement of the muscles has not been altered by the presence of a cheek pouch. If a group of squirrels is not mentioned in the discussion of a muscle, it is understood that the muscle in that group agrees in all essentials with the description of the standard.

Branchiomerer Musculature

MASTICATORY GROUP

Supplied by masticatory nerve

Masseter.—Synonyms: see Hill, 1937: 102-104. Tullberg (1899) and Kunstler (1887) described the masseter of *Sciurus vulgaris* and *Marmota marmota* in detail. The masseter of rodents is divisible into three main parts. Two of these are incompletely differentiated into two subdivisions.

Masseter superficialis.—Triangular sheet covering slightly more than ventral half of masseter lateralis profundus. Originates on masseteric tubercle by stout, narrow tendon, from which connective tissue sheath spreads fanwise over anterior two-thirds of muscle; some fibers attach to lateral surface of mandible anterior to masseteric fossa. Inserts on ventral and posterior margins of angular process except posterodorsal tip, and extends slightly on to medial surface. Similar but relatively longer in *Marmota* and *Cynomys*, due to posterior elongation of angular process. Originates in *Sciurus* by broader tendon from weak masseteric tubercle and depression between tubercle and P3; correlated with greater distance between infraorbital foramen and P3, resulting from more extensive masseter lateralis profundus pars anterior; insertion on margin of angular process broader, not merely expanded near posterodorsal tip as in terrestrial forms. Width of tendon at origin in *Tamiasciurus* intermediate between width in *Otospermophilus* and *Sciurus* but more like latter; insertion on angular process also intermediate in extent.

Masseter lateralis profundus pars anterior.—Arises mostly on anterior surface of zygomatic plate but posterior fibers arise from anterior tip of zygomatic arch and aponeurosis of pars posterior; fibers run posteroventrad. Inserts by heavy fascia on ventral masseteric crest and slightly posterior thereto and in lower part of masseteric fossa; narrow and pointed at dorsal end, nearly cylindrical at origin and flattened at insertion. Stoutest in subgenus *Citellus*, *Xerospermophilus*, and *Marmota*; stoutest in *Cynomys*. Weaker in *Neotamias* than in other sciurids. Origin more extensive in *Sciurus* than in terrestrial forms, because of greater expansion of zygomatic plate and greater depth of rostrum; blunt rather than pointed at dorsal end; fibers run more nearly vertically; tendon more clearly differentiated at anterior margin of insertion and ventral masseteric crest consequently higher. *Tamiasciurus* resembles *Sciurus*, but muscle not as broad at origin. Dorsal end of origin rounded in *Glaucomys*.

Masseter lateralis profundus pars posterior.—Arises from entire lateral surface of zygomatic arch and posterodorsal margin of zygomatic plate; anterior fibers run posteroventrad and posterior fibers run nearly posteriad. Inserts on lateral surface of angle except part occupied by masseter superficialis and pars anterior; posterior part extends lateral to ventral mandibular incisure and inserts on posterodorsal tip of angle by tendon. Incompletely divided into superficial and deep parts by aponeurosis which forms tendon that arises from posterodorsal margin of zygomatic plate; deep part more closely connected with pars anterior. Pars posterior larger than pars anterior in terrestrial forms and chipmunks and smaller in tree and flying squirrels. Pars posterior appears stoutest in subgenus *Citellus*, *Xerospermophilus*, and *Cynomys*, and weaker in *Ammospermophilus*. Origin on zygomatic arch less extensive in *Sciurus*, *Tamiasciurus*, *Neotamias*, and *Glaucomys*, in the first two because it is limited to the lower part of arch and in the latter because arch is weaker.

Masseter medialis pars anterior.—Originates on posterointernal surface of zygomatic plate and medial surface of zygomatic arch; fibers run nearly ventrad; inserts on dorsal

masseteric crest of mandible, between crest and origin of dilator of pouch on alveolar ridge, anterior part of base of coronoid process, and alveolar tubercle. No fibers pass through infraorbital foramen. Thicker in tree squirrels but insertion less extensive; inserts from point posterior to tip of dorsal masseteric crest to base of coronoid process; this correlated with untwisted condition of zygomatic arch and stronger dorsal masseteric crest. In *Glaucomys* origin is on entire orbital face of zygomatic plate; anterior fibers run posteroventrad.

Masseter medialis pars posterior.—Arises on medial surface of zygomatic process of squamosal; fibers converge anteroventrad to insert in fossa on lateral surface of condyloid process. Fibers run more nearly anteriad in tree and flying squirrels.

Temporalis.—Divisible into three parts. Anterior part small; originates along anterior half of parietal ridge internal to medial part; fibers converge posterior to postorbital process; inserts by tendon on anterolateral border of coronoid process. Medial part much larger than other parts; arises on parietal ridge, sagittal crest, anterior surface of superior nuchal line, upper part of squamosal, and greater part of parietal bone; fibers run anteroventrad to insert on medial surface and dorsal tip of coronoid process. Posterior part less extensive but heavier than anterior part; arises on ventral surface of squamosal; passes external to zygomatic process of squamosal; inserts on lateral surface of coronoid process. Origin less extensive in *Ictidomys*, *Callospermophilus*, and *Glaucomys*; still smaller in *Xerospermophilus*, *Ammospermophilus*, and *Neotamias*. Especially strong in larger species of subgenus *Citellus* and in *Cynomys*. In tree squirrels temporalis almost reaches middorsal line but is loosely attached to bone and does not cause the formation of parietal ridges. There is no apparent correlation between the sizes of temporalis muscle and coronoid process.

Pterygoideus externus.—Originates on anterolateral part of pterygoid fossa, lateral pterygoid plate, and alisphenoid; fibers run posterodorsolaterad; inserts on medial surface of condyloid process; fills space between condyloid process and tympanic bulla; much smaller than internal pterygoid. Appears to be larger in *Sciurus*; originates on distinct process on anterolateral part of pterygoid fossa. In comparison with internal pterygoid, stronger in *Neotamias* and *Glaucomys*; in latter arises on anterior surface of tympanic bulla up to inflated area below squamosal foramen.

INTERNAL PTERYGOID GROUP

Supplied by medial branch of mandibular nerve.

Pterygoideus internus.—Massive; arises in pterygoid fossa and in depression antero-medial to tympanic bulla; fibers run ventrolaterad; inserts in inferior pterygoid fossa of mandible. Larger in *Cynomys*. Area of origin smaller in tree squirrels; greatly reduced in *Glaucomys* and *Neotamias*. Assuming that degree of inflection of angle indicates strength of muscle, internal pterygoid is weakest in tree squirrels and strongest in *Cynomys*.

Tensor veli palatini.—Synonym: tensor palati, Edgeworth, 1935. Small; arises from anteromedial angle of tympanic bulla, posterodorsal to posterior part of internal pterygoid; fibers run ventromediad; inserts on soft palate, its tendon passing under ventral margin of medial pterygoid plate anterior to hamulus of pterygoid.

Tensor tympani.—Not dissected. According to Hill, 1937:105: "Arises from inner surface of bulla; attaches to manubrium mallei, near anterior process."

MYLOHYOID GROUP

Supplied by mylohyoid branch of mandibular nerve.

Mylohyoideus.—Synonym: intermandibularis posterior, Edgeworth, 1935. Originates in depression on dorsal side of medial surface of mandibular ramus below diastema and along mylohyoid line nearly to mandibular foramen; fibers run mediad and slightly posteroventrad; inserts on median raphe and anteroventral surface of body of hyoid dorsal to tendinous arch of digastric.

Transversus mandibularis.—Synonyms: transverse-maxillaire, Kunstler, 1887; inter-mandibularis anterior, Cords, 1918, Edgeworth, 1935. Runs transversely between ventro-medial margins of mandibular rami immediately posterior to symphysis. Situated ventral to anterior margin of mylohyoid and between anterior ends of anterior digastrics. Low crest present on ramus at origin.

Digastricus.—Synonym: biventer maxillae, Hoffmann and Weyenbergh, 1870. Posterior digastric is in hyoid constrictor group; discussed here for convenience.

Anterior digastric runs parallel to midventral line in contact with mate except at anterior end; external to mylohyoid and internal to sphincter colli profundus. Arises from ridge posterior to symphysis on ventral surface of ramus and in fossa medial to ridge. Becomes narrower at posterior end, where it unites with posterior digastric by long tendon; tendon parallels anterior horn of hyoid, inserting on ventral curve of body of hyoid near posterior margin and on tendinous arch. Tendon joining anterior and posterior parts of digastric extends as sheath over anterior surface of medial end of posterior digastric. Posterior digastric spindle-shaped; originates by strong and short tendon on paroccipital process; runs posterior to stylohyal cartilage and passes ventral to ceratohyal to end in conjoining tendon.

In one specimen of *C. mexicanus* some crossing over of fibers of left and right anterior digastrics occurs. Complex overlapping of medial fibers occurs in *Marmota flaviventer* but not in *Marmota marmota* (Kunstler, 1887). In *Callospermophilus*, *Sciurus*, *Tamiasciurus*, and *Marmota* the tendon joining anterior and posterior parts is short, seemingly because of larger posterior part. In *Glaucomys* posterior digastric almost as large as anterior; tendon short; tendinous arch situated well in front of body of hyoid and anterior digastric has no attachment to hyoid.

CONSTRUCTOR COLLI GROUP

(Figs. 44-47).

Supplied by superficial branches of facial nerve. The muscles of *Sciurus* are taken as the standard in this group.

According to Huber (1930) the primitive sphincter colli, the homologue of the sphincter colli of reptiles, has given rise to the platysma and the sphincter colli profundus of placental mammals. These two primitive muscle layers invaded the face and subsequently developed into the many superficial facial muscles. The platysma, arising in the nuchal region, gives rise to the platysma proper, postauricularis, antitragicus, helcis, and mandibuloauricularis. The sphincter colli profundus has formed the sphincter colli profundus proper, sternoauricularis, tragohelecinus, interscutularis, preauricularis, depressor helcis, auriculolabialis, orbicularis oculi, nasolabialis, maxillolabialis, maxillonasalis, orbicularis oris, and buccinatorius. In some placental mammals a remnant of the primitive sphincter colli occurs as a band of fibers encircling the neck, and ventral bundles of it may overlap the platysma to form a sphincter colli superficialis. This interpretation of the evolution of the facial muscles in mammals is accepted in this study.

Sphincter colli primitivus and *sphincter colli superficialis*.—In some specimens a few fibers are present which may be doubtfully referred to these muscles; usually absent.

Platysma.—Synonyms: superficial panniculus in the neck, Parsons, 1894; platysma et peaucier de la nuque (part), Alezais, 1900; platysma (part), Sleggs, 1926. This is the platysma of most authors, but the name is also applied to the platysma plus the sphincter colli profundus.

A thin sheet of fibers closely adherent to subcutaneous fascia of side of head and neck. Separable into dorsal and ventral parts. Dorsal part inserts by three divisions: platysma 1 by broad aponeurosis on middorsal line from occiput nearly to interscapular fossa, anterior part of insertion covered by posterior part of postauricularis; platysma 2 is ventral to and indistinctly separated from platysma 1, inserts in fascia external to upper part of scapula; platysma 3 composed of scattered fibers in skin of neck and shoulder and of head posterior to pinna; in area posteroventral to pinna platysma 1-3 merge into a single sheet, called body of platysma, which passes ventral to pinna and

zygoma and external to masseter to unite with mystachial pad and also with orbicularis oris about angle of mouth; no attachment to skeleton. Ventral part (platysma 4) strap-shaped; not completely separable from platysma 2 and posterior part of body of platysma; arises from orbicularis oris lateral to midventral line and runs posterodorsolaterad below body of platysma to insert in fascia anterior to ventral half of scapula; seemingly homologous to mandibulolabialis of some rodents (Schreiber, 1929).

In *Glaucomys* platysma 2 is a distinct slip inserting on thenar pad; it runs beneath skin of lateral surface of arm and over shoulder to point of mergence with platysma 1; this is a unique specialization to pull skin of arm and shoulder laterad to increase surface for gliding. Platysma 3 weaker than in other sciurids. Platysma 4 inserts in skin of neck between shoulder and base of ear.

In *Marmota* platysma 1 less extensive in origin; much weaker than platysma 3, which spreads as heavy sheet over upper surface of neck and over shoulder to interscapular fossa. Platysma 2 continuous with platysma 3; extends across side of neck and ventral part of scapula to attach by fascia about lateral surface of elbow; a distinctive fossorial adaptation. Platysma 4 attaches on posterior margin of metacromion; otherwise as in *Sciurus*. A division not present in *Sciurus* arises in upper lip internal to attachment of body of platysma and merges with platysma 4 posterior to external part of sphincter colli profundus.

In other terrestrial squirrels and chipmunks platysma similarly modified by presence of cheek pouches. A division which is continuous posteriorly with platysma 4, originates on posterior margin of metacromion dorsal to attachment of platysma 4 and inserts on posterolateral surface of cheek pouch; called lateral retractor and discussed in connection with cheek pouch. Platysma 1 especially strong in *Otospermophilus*, *Callospermophilus*, and *Cynomys*; reduced to thin band originating on spine of axis in *Ammospermophilus*; in other groups intermediate in size between that in *Sciurus* and *Ammospermophilus* and less extensive at origin than in *Sciurus*. Platysma 2 separate from platysma 1; stouter in ground squirrels, except *Poliocitellus* and subgenus *Citellus*, and chipmunks than in tree squirrels. Platysma 3 stouter in ground squirrels, except *Poliocitellus*. Platysma 4 as in *Sciurus*, except posterior end attaches to metacromion as in *Marmota*.

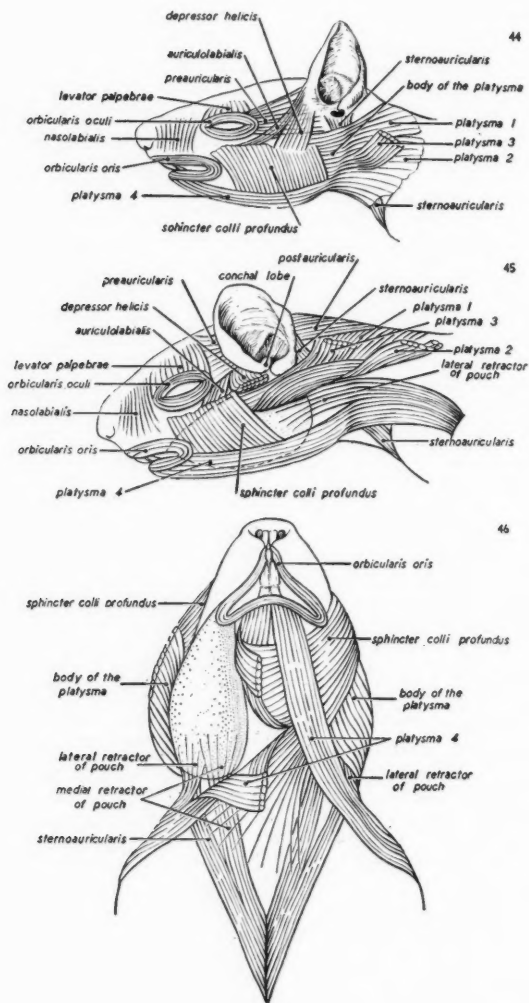
In comparison with the primitive plan of *Sciurus* the platysma is most highly specialized in *Glaucomys* and *Marmota*, probably in correlation with volant and fossorial habits. There is a tendency toward stronger development of platysma 3 in terrestrial forms. The posterior attachment of platysma 4 has shifted from the subcutaneous fascia of the shoulder to the metacromion in those sciurids which possess cheek pouches, and a special retractor of the pouch is fully differentiated in all of these forms except *Marmota*, in which the differentiation is incomplete.

Sphincter colli profundus.—Synonyms: decussating fibers of superficial panniculus on ventral surface of neck (external layer) and deep panniculus or sterno-facialis (internal layer), Parsons, 1894; platysma et peaucier de la nuque (part) Alezais, 1900.

Composed of external and internal layers. External layer ends dorsally in fascia below zygoma from point slightly anterior to pinna to level of angle of mouth; a thin sheet situated internal to depressor helcis, external to body of platysma and most of fibers of auriculolabialis, and internal to platysma 4 except a few fibers immediately posterior to chin; fibers run transversely in anterior part of posteroventromedial in middle and posterior parts, decussate over ventral surface of neck and throat and end in fascia of hindneck and breast. Internal layer arises in fascia between upper part of masseter and body of platysma; fibers pass posteroventromedial internal and nearly at right angles to decussating fibers of external layer to converge on ventral surface of sternum and adjacent parts of breast.

In *Glaucomys* external layer weak, limited to anterior half of throat and extends dorsad little beyond platysma 4; anterior fibers form transverse band external to anterior end of platysma 4. Internal layer heavier than in *Sciurus* but origin not as extensive; ends dorsally in fascia below anterior half of zygoma.

External and internal layers in other sciurids heavier than in tree squirrels. External layer less extensive at dorsal attachment, ending posteriorly at level of genal vibrissae;



decussating fibers run ventral to platysma 4 of opposite side; especially heavy in *Policitellus*, *Xerospermophilus*, and *Ammospermophilus*; anterodorsal fibers form a distinct band near angle of mouth which band curves around external surface of orifice of cheek pouch and ends internal to nasolabialis. Internal layer arises on lateral surface of cheek pouch, except in *Marmota* and *Cynomys*, and on throat medial to pouch; closely attached to pouch by fascia; fibers run posteroventromedial and most of them converge at posteromedial angle of pouch to form a definite muscle which attaches to ventral surface of first two sternebrae, which muscle called medial retractor and further discussed in connection with cheek pouch. Some fibers spread out above and below medial retractor and end in fascia of throat and breast. In *Marmota* and *Cynomys* internal layer a continuous sheet from midline of breast, ventral to first two sternebrae, to fascia along dorsal margin of masseter muscle; more extensive than in forms with well developed cheek pouches. In *Cynomys* a medial retractor is weakly differentiated from anterior fibers of sheet.

Postauricularis.—Synonym: cervico-auriculo-occipitalis, Schreiber, 1929. Composed of superficial and deep layers. Superficial layer originates on middorsal line from posterior part of skull to fourth or fifth cervical vertebra; anterior part is external to anterior part of platysma 1; fibers extend anterolaterad to insert on anterior two-thirds of medial surface of pinna below antihelix and on skin anteromedial to base of pinna. Deep layer narrower than superficial; originates partly internal and partly anterior to superficial layer; inserts on posterior half of base of pinna; fibers run transversely. In *Glaucomys* origin of superficial layer extends posteriad nearly to interscapular notch; covers part of trapezius. Size of muscle in direct ratio to size of ear. In forms with large ears part inserting on skin often a distinct slip, called occipitalis.

Sternoauricularis.—Synonyms: sterno-facial, Alezais, 1900; sphincter colli profundus pars auricularis, Schreiber, 1929; sternofascialis, Peterka, 1937. Originates ventral to first two sternebrae, posterior to origin of internal part of sphincter colli profundus, and on adjacent fascia; runs anterodorsad internal to platysma and external to parotid gland; inserts on base of ear posterior and ventral to intertragal notch. Clearly derived from sphincter colli profundus and not distinct from its near origin. Absent in *Glaucomys*. Not separated from sphincter colli profundus in *Cynomys* and few fibers attach to ear. In squirrels with cheek pouches, other than *Cynomys* and *Marmota*, parallels posterior part of medial retractor for short distance.

Interscutularis.—Synonym: interscutulatus, Hill, 1937. Represented by a few fibers extending transversely between anterior margins of pinnae in subcutaneous fascia; not consistently discernible in any species examined.

Preauricularis.—Synonyms: frontalis, Parsons, 1894; frontoauricularis, Schreiber, 1929. Originates on frontal bone anterior and dorsal to postorbital process; inserts on anterior part of base of pinna and on skin dorsal and ventral thereto; fibers interdigitate at insertion with those of postauricularis and auriculolabialis. In *Glaucomys* origin on frontal bone more extensive.

Antitragicus.—A minute muscle extending from dorsal part of cartilage of antitragus to ventral surface of cartilage of conchal lobe.

Helicis.—A small muscle imbedded in margin of folded anterior part of pinna; extends from level of antihelix into conchal lobe, where it bends posterodorsad to end in ridge passing from posterior tip of conchal lobe towards antihelix; individually variable in size.

Tragohelicinus.—About size of helicis; arises from cartilage ventral to intertragal notch and extends anterodorsad to cartilage at base of conchal lobe.

Mandibuloauricularis.—Originates on border of ventral mandibular incisive anterior to posterodorsal tip of angular process; runs dorsal and slightly posteriad internal to preauricular branches of facial nerve and on anterior surface of external auditory meatus; inserts on cartilage at base of conchal lobe. In *Ictidomys*, *Xerospermophilus*, *Ammospermophilus*, and *Callospermophilus* origin limited to inner side of anterodorsal tip of angular process. Origin nearer base of condyloid process in *Marmota*. Absent (?)

in *Cynomys*; Schreiber (1929) records the presence of a small mandibuloauricularis muscle in *C. l. ludovicianus*.

Depressor helcis.—Originates on cartilage of conchal lobe and fascia anterior thereto; closely associated with preauricularis and auriculolabialis at origin; fibers run ventrad in thin sheet external to dorsal part of body of platysma; inserts in fascia from genal vibrissae to level of posterior margin of pinna. Weak in *Xerospermophilus*, *Neotamias*, and *Marmota*, the fibers barely reaching dorsal margin of platysma.

Auriculolabialis.—Synonym: zygomaticus, Hoffmann and Weyenbergh, 1870. Arises anterior to dorsal part of base of pinna, mostly medial to posterior part of preauricularis; runs anteroventrad between eye and genal vibrissae, chiefly internal to anterior end of body of platysma, to merge with orbicularis oris and mystachial pad. In *Glaucomys* fibers terminate below the eye in subcutaneous fascia and on outer surface of body of platysma. In *Ammospermophilus* and *Ictidomys* fibers intermingle with those of anterior part of body of platysma and superficial layer of sphincter colli profundus; they do not reach orbicularis oris or mystachial pad. In ground squirrels more fibers appear to be external to body of platysma than internal.

Orbicularis oculi.—Synonym: orbicularis palpebrarum, Hoffmann and Weyenbergh, 1870, Parsons, 1894. Originates on anterior part of supraorbital crest, hamulus of lacrimal, and fascia of eyelids; forms band around eye; some fibers pass dorsad and ventrad from anterior margin to intermingle with fibers of nasolabialis and external part of sphincter colli profundus, these fibers sometimes called preorbicularis; similarly, fibers from posterior angle merge with those of preauricularis, these fibers from posterior angle merge with those of preauricularis, these fibers sometimes called postorbicularis. In *Cynomys* ventral part of preorbicularis strong; extends as special division on external surface of body of platysma.

Nasolabialis.—Synonyms: levator labii superioris, Parsons, 1894, Schreiber, 1929; levator labii, Peterka, 1937. Trapezoidal in outline; fibers nearly vertical. Arises on dorsal margin of zygomatic plate and on dorsolateral ridge of rostrum forward nearly to tip of nasal bone; some fibers merge with orbicularis oculi; inserts in mystachial pad and adjacent parts of upper lip. Rostrum shallower in terrestrial squirrels and chipmunks and nasolabialis correspondingly shallow.

Maxillolabialis.—Thin plate of vertical fibers internal to and incompletely separable from nasolabialis. Originates on ridge of maxilla lateral to incisor; inserts on upper lip dorsal and posterior to alveolus of incisor. In terrestrial squirrels more closely united with nasolabialis.

Maxillonasalis.—Synonym: dilator naris, Peterka, 1937. Triangular, narrower at insertion than at origin. Originates on premaxillary-maxillary suture at anterior margin of zygomatic plate and ventrally as far as dorsal margin of infraorbital foramen, internal to masseter lateralis pars anterior; runs antierad and slightly dorsad to insert at dorso-lateral angle of naris and in cartilage of dorsal border of naris; no tendon.

A Y-shaped muscle in other sciurids, except *Tamiasciurus* and *Glaucomys*. Dorsal head arises from projecting ledge of zygomatic plate anterior to lacrimal bone, thus partly responsible for concavity of zygomatic plate; ventral head originates on dorsal rim of infraorbital foramen; joins dorsal head near anterodorsal border of zygomatic plate, from whence tendon continues to insertion. Ventral head larger in *Neotamias*; passes through infraorbital foramen dorsal to infraorbital nerve and inserts on orbital margin of foramen; accounts for relatively larger size of foramen in chipmunks than in other squirrels.

Orbicularis oris.—Originates on rostrum near alveoli of incisors, from median line ventral to nostrils, and from mandible; runs in lips external to cheek pouch; part forms an arch about bases of lower incisors.

Buccinatorius.—Arises on incisive ridge of rostrum internal to other muscles. Passes ventrad as sheet of fibers on side of rostrum. Anterior fibers merge with orbicularis oris

of upper lip. Posterior fibers of sheet bend around angle of mouth, external to buccal epithelium; some fibers spread ventrad to dorsomedial margin of diastema of ramus (see ventral muscles of cheek pouch), while other posterior fibers connect the alveolar ridges and end in depression between base of coronoid process and M_2 (see dilator of cheek pouch). A small band of fibers separates from division to ramus and runs dorsad to attach ventral to infraorbital foramen. Cheek pouches in sciurids form in buccinator, resulting in specialization of various parts; these parts discussed in connection with cheek pouch.

Cheek pouch. (figs. 45-47).—Absent in *Sciurus*, *Tamiasciurus*, and *Glaucomys*, in other sciurids opens into vestibulum oris by vertical, crescentic orifice slightly anterior to cheek teeth and posterior to angle of mouth. Pouch forms as evagination from vestibulum oris into buccinator; pushes posteriad internal to platysma and sphincter colli profundus, which are altered in correlation with its development. Intrinsic muscles not studied; described in *Citellus richardsonii* by Sleggs (1926). Orbicularis oris covers external margin of orifice and aids in closing it.

In *Marmota* the rudimentary cheek pouch is situated mostly dorsal to angle of mouth. Has three extrinsic muscles which are derived from buccinator: 1) Arises in depression between coronoid process and M_3 ; runs lateral to cheek teeth and attaches to alveolar ridges; inserts on internal surface of cheek pouch in front of plane of fourth premolars; enlarges orifice and anterior end of pouch and is called dilator; this part of buccinator well developed in forms without pouches. 2) Small; originates on dorsomedial margin of diastema of ramus; fibers run dorsad; divides into two parts at ventral margin of pouch, outer part inserting on lower half of external surface of pouch back of orbicularis oris, inner part inserting on internal surface up to dorsal margin of pouch; called ventral muscle of pouch; homologous to posteroventral part of buccinator of *Sciurus*. 3) Small; arises in fossa posterior to alveolus of upper incisor; runs posteroventrad to insert on anterodorsal margin of pouch behind orbicularis oris; called dorsal muscle of pouch; relatively smaller than in other forms with pouch. Cheek pouch larger in other terrestrial squirrels and chipmunks, with three muscles described for *Marmota* and further

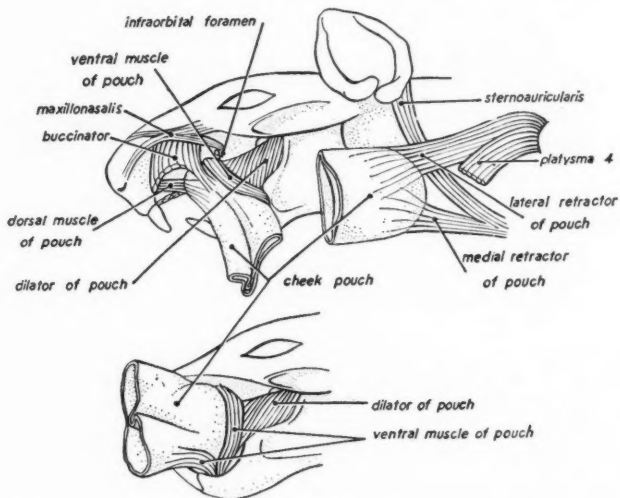


Fig. 47. Musculature of the cheek pouch of *Citellus* (*Otospermophilus*) *variegatus* ($\times 2\frac{2}{3}$).

specialization of extrinsic muscles. 4) Medial fibers of internal part of sphincter colli profundus form separate muscle; originates on ventral surface of first two sternbrae; inserts on external and internal surfaces of posteromedial part of pouch; called medial retractor. Remainder of internal part of sphincter colli profundus spreads over pouch and closely attaches to it by fascia. 5) Muscle differentiates from dorsal part of posterior half of platysma 4; originates on metacromion dorsal to origin of platysma 4 and is incompletely separated from it near origin; runs parallel to platysma 4 to insert on external surface of posterolateral region of pouch; called lateral retractor. Body of platysma in contact with external surface of dorsal part of pouch but no fibers directly connected to it. A few fibers sometimes run to cheek from lateral surface of pouch posterior to orifice.

Cheek pouch small (sizes based on fully extended condition) in *Cynomys*, ending posteriorly below eye; medial retractor poorly differentiated. Slightly larger in *Xerospermophilus*, terminating in front of level of pinna; retractors correspondingly small. Of medium size in *Ictidomys* and subgenus *Citellus*, ending below pinna. Large in *Otospermophilus*, *Ammospermophilus*, *Callospermophilus*, *Poliocitellus*, and *Neotamias*, extending posteriorly to level of manubrium sterni; medial retractor unusually large in *Poliocitellus*.

HYOID CONSTRICTOR GROUP

Supplied by stylohyoid branch of facial nerve.

Digastricus posterior.—Described in connection with digastricus anterior (page 310).

Stylohyoideus.—Small, spindle-shaped. Originates by tendon nearly as long as body on anterior face of stylohyal cartilage except distal tip and by a few fibers on connective tissue covering tympanic bulla; runs ventromedial ventral to stylohyal cartilage and internal to posterior digastric; inserts by short tendon on anteroventral surface of posterior process and on ventral surface of shoulder of hyoid. In tree and flying squirrels origin is by fascia rather than by distinct tendon; insertion by tendon nearly as long as body. In *Neotamias* tendons at origin and insertion are short.

Jugulohyoideus.—Arises from paroccipital process and jugular notch; incompletely separable from posterior digastric; fibers run transversely to length of body of muscle; inserts on posterior surface of stylohyal cartilage opposite origin of stylohyoideus. Separation from posterior digastric complete in some individuals of other ground squirrels but usually as in *Otospermophilus*. Distinct muscle in *Sciurus*, *Tamiasciurus*, and *Glaucomys*; inserts nearer distal end of stylohyal cartilage.

GLOSSOPHARYNGEAL GROUP

Supplied by glossopharyngeal nerve.

Stylopharyngeal.—Arises on posterodorsal surface of stylohyal cartilage near proximal end; situated dorsal to insertion of jugulohyoideus; runs medial to insert on dorso-lateral wall of thyroid cartilage and adjacent parts of pharynx.

The other muscles supplied by the glossopharyngeal nerve and the pharyngeal and laryngeal muscles innervated by the vagus and spinal accessory nerves were not studied.

TRAPEZIUS GROUP

Supplied by accessory and second and third spinal cervical nerves. There is doubt as to whether the muscles of this group are referable to the branchiomic series or whether they are of both branchiomic and myomeric origin (Nishi, 1922).

Sternomastoideus.—Body V-shaped in transverse section with groove opening laterally for reception of cleidomastoideus; divided into two separate bands in some specimens. Originates on flattened anterior surface of manubrium sterni (sternomastoid fossa); runs anterodorsad and slightly laterad ventral to cleido-occipitalis; inserts by fascia on ventro-lateral angle of mastoid process and on ventral tip of superior nuchal line. Arises on

dorsal surface of point of manubrium sterni in tree squirrels, and on cranioventral surface of Y-shaped manubrium sterni and on sternal end of clavicle in flying squirrels.

Cleidomastoideus.—Situated partly internal to cleido-occipitalis and sternomastoideus. Arises on sternal one-fourth of cranial surface of clavicle, partly medial and partly dorsal to origin of cleido-occipitalis; runs parallel to and inserts in common with sternomastoideus. In *Glaucmys* origin is broader and entirely dorsal to origin of cleido-occipitalis.

Cleido-occipitalis.—Synonym: clavotrapezius, Peterka, 1937. Originates on ventral surface of clavicle partly lateral to origin of cleidomastoideus; runs craniodorsolaterad on side of neck internal to platysma; either adjoins or fuses with anterior part of acromiotrapezius; inserts by aponeurosis on superior nuchal line down to dorsal edge of mastoid. Completely separated from acromiotrapezius in *Marmota* and *Cynomys*; especially heavy in *Marmota*. Inserts farther ventrally in *Glaucmys* and is external to anterior ends of sternomastoideus and cleidomastoideus.

Trapezius.—Synonym: cucullaris, Hoffmann and Weyenbergh, 1870. A single sheet with acromial and spinal parts. Originates from medial part of superior nuchal line, on middorsal line caudad to level of first lumbar vertebra, and on lumbodorsal fascia.

Acromiotrapezius.—Synonyms: anterior portion of trapezius, Parsons, 1894; trapèze antérieur, Alezais, 1900. Cranial part situated internal to platysma 1; ventral border in contact with cleido-occipitalis or fused with it. Fibers run caudoventrad in cranial part and increasingly more nearly ventrad toward caudal margin at level of seventh thoracic vertebra. Fibers converge to insert on lateral surface of metacromion, proximal part of acromion, and crest of scapular spine except dorsal one-fourth; insertion situated internal to omocervicalis, platysma 4, and lateral retractor of pouch. No attachment to acromion in *Amnospermophilus*, *Neotamias*, *Sciurus*, and *Tamiasciurus*; insertion limited to scapular spine and fossa on metacromion; metacromion relatively smaller in these squirrels. Insertion covers entire lateral surfaces of reduced metacromion and acromion in *Glaucmys*.

Spinotrapezius.—Synonyms: posterior portion of trapezius, Parsons, 1894; trapèze postérieur, Alezais, 1900. Smaller than acromiotrapezius. Runs craniad and slightly ventrad from origin to insert on scapular spine in common with dorsal one-third of acromiotrapezius. In *Marmota* a small slip separates from caudal part and runs to skin on dorsolateral part of neck.

Myomeric Musculature

OCULAR MUSCLES

The ocular muscles, supplied by the third, fourth, and sixth cranial nerves, do not differ from the general mammalian arrangement.

LINGUAL MUSCLES

Supplied by hypoglossal nerve

Genioglossus. Arises on mandible posterior to symphysis and dorsal to origin of geniohyoid; a vertical band spreading fanwise; fibers attach to ventromedial surface of tongue; extends posteriad to point posterodorsal to body of hyoid, to which it attaches by fascia.

Hyoglossus. Originates dorsal to geniohyoid on anterior surface of body of hyoid, on ventral surface of shoulder of hyoid, and on anterior surface of proximal end of posterior process of hyoid; fibers run anterolaterad; inserts on side of tongue near base and along side of tongue anterior thereto. Relatively larger in *Sciurus*, *Tamiasciurus*, and *Neotamias*; arises from midline of anterior surface of body of hyoid to distal end of anterolateral surface of posterior process.

Styloglossus. Arises from anterior surface of stylohyal cartilage and often from

distal end of ceratohyal bone dorsal to insertion of stylohyoid; fibers run anteroventro-mediad, parallel to ceratohyal, and bend anteriorly external to hyoglossus and internal to mylohyoid; inserts on side of tongue.

Muscles of the Body

DORSAL DIVISION

The dorsal muscles of the body are supplied by branches of the dorsal rami of the spinal nerves.

SUPERFICIAL SPINO-OCCIPITAL GROUP

Splenius.—Arises from nuchal ligament and by tendons from tips of neural spines of first two thoracic vertebrae; fibers run craniad and cranioventrolaterad; inserts on entire caudal margin of superior nuchal line, internal to insertion of occipitoscapularis, down to dorsolateral tip of mastoid. Ventral part incompletely differentiated from dorsal part near insertion and attached to mastoid by small tendon.

SACROSPINALIS GROUP

Sacrospinalis.—Arises on crest and dorsal margin of ilium and on spinous processes of sacral and lumbar vertebrae; inserts by fibers on transverse processes of lumbar vertebrae.

Iliocostalis.—Lumbar part arises from cranial and lateral parts of sacrospinalis and inserts on last six ribs. Dorsal part arises on third through sixth ribs and inserts on first five ribs. Cervical part arises on first four ribs and inserts on last three cervical vertebrae and first three ribs.

Longissimus.—Dorsal part arises from craniomedial part of sacrospinalis; inserts on last ten ribs, on accessory processes of caudal thoracic and cranial lumbar vertebrae, and on transverse processes of cranial thoracic vertebrae. Cervical part arises in continuity with dorsal part; inserts on transverse processes of last three cervical vertebrae. Cephalic part arises from transverse processes of cervical vertebrae; inserts on superior nuchal line at dorsal margin of mastoid.

Extensor caudae lateralis.—Continuous with dorsal part of longissimus. Some fibers arise from accessory processes of lumbar vertebrae but most of fibers arise from transverse processes of last two or three sacral vertebrae and from several of proximal caudal vertebrae; inserts on dorsal and lateral surfaces of articular processes of caudal vertebrae. Presacral part appears stronger in forms with larger tails.

Spinalis dorsi.—Incompletely differentiated. Originates on spinous processes of most of thoracic and first few lumbar vertebrae; interconnects spinous processes of cranial thoracic vertebrae and last five or six cervical vertebrae.

SEMISPINALIS GROUP

Semispinalis capitis.—Caudal part nearly vertical and cranial part nearly horizontal; meets mate in midline dorsal to cervical vertebrae. Arises on dorsal surfaces of transverse processes of last six cervical and on first four to seven thoracic vertebrae; fibers run craniad; inserts on caudoventral surface of superior nuchal line from midline to a small tuberosity located at posterior end of parietal-squamosal suture. Clearly divisible into dorsomedial part (biventer cervicis of authors) and ventrolateral part (complexus of authors) near caudal end; the two parts not clearly separable near skull. Dorsomedial part inserts by fibers on skull and on aponeurosis by which ventrolateral part inserts. Two parts clearly separable in tree squirrels and chipmunks and indistinguishable in flying squirrels.

Semispinalis.—Not separable into cervical and dorsal parts and indistinguishable from multifidus and rotatores. Arises from mamillary processes of first two sacral,

lumbar, and last four or five thoracic vertebrae, and from dorsal surfaces of transverse processes of other thoracic vertebrae; inserts on spinous processes of last six cervical, thoracic, and lumbar vertebrae. Most of fibers in lumbar and sacral regions pass over three segments, but some fibers pass over two and some over one segment. The more anterior fibers pass over more than three segments.

Extensor caudae medialis.—Continuous with semispinalis. Arises from spinous processes of sacral and first four or five caudal vertebrae; inserts by slender tendons on transverse processes or on cranial surfaces of cranial articular processes of vertebrae caudal to origin.

SUBOCCIPITAL GROUP

Rectus capitis posterior.—Situated ventral to semispinalis capitis and dorsomedial to longissimus capitis. Arises from entire dorsal margin of spine of axis and dorsal surface of dorsal arch of atlas; fibers diverge from origin to insert on occiput from midline to level of paroccipital process. Completely divisible into major and minor parts in *Marmota*.

Obliquus capitis inferior.—Situated lateroventral to origin of rectus capitis posterior and posterior to rectus capitis lateralis; covered ventrolaterally by splenius. Originates on lateral surface of spine and dorsal surface of dorsal arch of axis; inserts in depression on dorsolateral margin of wing of atlas.

Obliquus capitis superior.—Arises on anteroventral margin of wing of atlas; runs cranial; inserts on mastoid ventrolateral to mastoid foramen and on dorsal part of posterior surface of paroccipital process.

Longus atlantis.—Situated lateral to origin of semispinalis capitis and dorsal to origin of levator scapulae. Arises by separate small slips from transverse processes of second through fifth cervical vertebrae; inserts by tendon on posterolateral angle of wing of atlas.

VENTRAL DIVISION

The skeletal muscles of the body and appendages, which have not been previously discussed, are included in the ventral division. These muscles are supplied by branches of the ventral rami of spinal nerves.

CERVICAL PREVERTEBRAL GROUP

Rectus capitis anterior.—Synonym: rectus capitis anticus minor, Hoffmann and Weyenbergh, 1870, Parsons, 1894. Arises from ventral arch of atlas lateral to attachment of atlantoscaphularis ventralis; runs anteromedial; inserts in fossa on ventral surface of basioccipital bone anterior to occipital condyle.

Longus capitis.—Synonym: rectus capitis anticus major, Parsons, 1894. Arises chiefly from enlarged costal element of transverse process of sixth cervical vertebra and from costal elements of fourth and fifth cervical vertebrae; runs anteriorly lateral to esophagus and dorsal to internal carotid artery; inserts by tendon on tuberosity of basioccipital, which is situated posterior to basisphenoid-basioccipital suture and medial to tympanic bulla, and by fibers in depression in anterior part of ventral surface of basioccipital.

Longus colli.—Composed of two parts. Cranial part arises from ventral surfaces of transverse processes and bodies of third through sixth cervical vertebrae; inserts on ventral tubercle of atlas. Caudal part arises from first two ribs and from lateroventral surfaces of seventh cervical vertebra and first three thoracic vertebrae; inserts on caudal process of costal element of sixth cervical vertebra.

CAUDAL FLEXOR GROUP

Flexor caudae lateralis.—Arises from last lumbar and from sacral and caudal vertebrae; inserts on ventral surfaces of caudal vertebrae and on chevron bones of tail.

Flexor caudae medialis.—Arises from ventral surfaces of transverse processes and bodies of last two or three sacral and first few caudal vertebrae; inserts on ventral surfaces of caudal vertebrae and on chevron bones of tail.

MEDIAL VENTRAL CERVICAL GROUP

Geniohyoid supplied by hypoglossal nerve. Infrahyoid muscles supplied by special nerve from loop between first and second cervical nerves, independent of hypoglossal.

Geniohyoideus.—In contact with mate along medial margin; situated dorsal to mylohyoid and transverse mandibular muscles. Arises in shallow fossa posteromedial to alveolus of lower incisor; fibers run posteriad; inserts on middle of anterior surface of body of hyoid.

Sternohyoideus.—In contact with mate in midventral line. Originates in depression on dorsal side of manubrium sterni; fibers run cranial; inserts on posteroventral surface of body of hyoid.

Sternothyroideus.—Arises on dorsal side of manubrium and fascia of sternohyoid; runs ventrolateral to trachea; inserts on side of thyroid cartilage near anterior margin.

Thyrohyoideus.—Synonym: hyo-thyroideus, Hoffmann and Weyenbergh, 1870. Arises from thyroid cartilage in contact with insertional end of sternothyroid; inserts on posteromedial surface of posterior process of hyoid.

Omoxyoideus.—Originates in notch dorsal to coracoid process on cranial border of scapula; runs cranioventromedial across neck; inserts on body of hyoid dorsolateral to insertion of sternohyoid.

MEDIAL THORACOABDOMINAL GROUP

Rectus abdominis.—Synonym: grand droit de l'abdomen, Alezais, 1900. Attaches cranially on caudoventral surface of sternal half of first costal cartilage, ventrolateral surface of manubrium and lateral surface of sternal half of first costal cartilage, ventrolateral surface of manubrium and lateral surface of its caudal process, sternal end of second rib, and on third rib. Passed caudad internal to pectoralis and external to costal cartilages as far as caudal end of xiphisternum. From this point it contacts mate along linea alba. Attaches caudally to pubic symphysis or symphyseal ligament and adjacent parts of pelvis. In some individuals the cranial attachment is limited to caudoventral surface of sternal half of first costal cartilage and ventrolateral surface of manubrium sterni; this condition appears to be normal in *Marmota*. Broader cranially in tree squirrels; attaches to entire caudoventral surface of first costal cartilage and by fascia to second costal cartilage. In *Glaucomys*, attaches only to caudolateral margin of manubrium sterni and to first costal cartilage; crest of manubrium correspondingly smaller.

LATERAL CERVICAL GROUP

Rectus capitis lateralis.—Arises on anterior part of lateral margin of wing of atlas, lateral to origin of obliquus capitis inferior; runs craniodorsad; inserts in fossa lateral to mastoid foramen, on lateral part of exoccipital, and on medial half of paroccipital process.

Scalenus.—Composed of dorsal and ventral parts. Ventral part small; arises by tendons from ventral surfaces of transverse processes of second through seventh cervical vertebrae and cranial surface of sternal end of first rib; slips converge cranially and insert on tendon of dorsal part. Dorsal part inserts by stout tendon on wing of atlas ventral to caudal end of vertebral canal; at level of first and second ribs it divides into three slips to third, fourth, and fifth ribs; slips to third and fourth ribs pass external to slips of serratus anterior that attach to third and fourth ribs; slip to fifth rib lies internal to the cranial slip of external oblique, which attaches to fourth rib.

LATERAL THORACOABDOMINAL GROUP

Obliquus abdominis externus.—Arises from lumbodorsal fascia and by slips from caudolateral surfaces of third to fifth (usually fourth) through twelfth ribs, interdigitating with slips of serratus anterior caudal to fourth rib; fibers run caudoventrad; inserts on sheath of rectus abdominis from level of xiphisternum to inguinal ligament.

Obliquus abdominis internus.—Arises from lumbodorsal fascia from level of caudal margin of serratus posterior inferior to crest of ilium and also from inguinal ligament; fibers run cranioventrad; inserts on caudal margins of caudal costal cartilages and on linea alba by an aponeurosis that fuses with aponeurosis of external oblique and transverse abdominal. Continuous with internal intercostals.

Transversus abdominis.—Arises from lumbodorsal fascia deep to internal oblique and from costal cartilages at caudal margin of thorax; fibers run medialis and slightly caudad; inserts on inguinal ligament and on linea alba by aponeurosis situated on inner surface of rectus abdominis.

Serratus posterior superior.—Arises by aponeurosis on middorsal line from about seventh cervical to eighth thoracic vertebra. Fibers run caudoventrad. Inserts by seven or eight slips on cranial borders of angles of third or fourth through tenth ribs; first five slips insert internal to serratus anterior; last two slips insert internal to slips of serratus posterior inferior that go to eighth and ninth ribs.

Serratus posterior inferior.—Slips longer than those of serratus posterior superior; arises by long aponeurosis from middorsal line approximately from level of ninth thoracic vertebra to level of third lumbar vertebra; inserts on caudolateral surfaces of eighth through eleventh ribs. Slip to eighth rib absent in *Xerospermophilus*, *Callospermophilus*, and *Cynomys*.

Subcostales.—Arise from pleural surfaces of all except first few ribs and from transverse processes of first one or two lumbar vertebrae; insert on caudal surface of dorsal parts of ribs.

Levatores costarum.—Arise from transverse and accessory processes; run caudoventrad; insert on ribs near angles.

Transversalis thoracis.—Arises on internal surface of sternbrae and on xiphisterum; inserts on most of costal cartilages.

Appendicular Musculature

The limbs of *Glaucomys*, *Sciurus*, *Tamiasciurus*, *Neotamias*, and *Ammodontomys* are long and slender, and the tendons of the long extensors and flexors are correspondingly longer than in other Nearctic sciurids.

MUSCLES OF THE PECTORAL GIRDLE AND LIMB

EXTENSOR SYSTEM

COSTO-SPINO-SCAPULAR GROUP

Levator scapulae and *serratus anterior*.—Synonyms: levator anguli scapulae and serratus, Hoffmann and Weyenbergh, 1870; levator anguli scapulae and serratus magnus, Parsons, 1894; angulaire and grand dentelé, Alezais, 1900; levator scapulae and serratus magnus, Peterka, 1937.

Levator scapulae and serratus anterior closely united into single layer near insertions and not clearly separable near origins. Arise by slips from caudal surface of wing of atlas dorsal to attachment of scalenus, tip of transverse process of third cervical vertebra, ventral tubercles of transverse processes of last four cervical vertebrae, and cranioventral surfaces of sternal ends of first eight ribs. Slips to cervical vertebrae and first four ribs are internal to scalenus; slips to fifth through eighth ribs interdigitate with slips of external oblique. Fibers converge dorsad, internal to scapula. Inserts on costal margin

of vertebral border of scapula and adjacent costal surface. Number of slips to ribs in groups other than *Otospermophilus* as follows: seven in subgenus *Citellus*, *Ictidomys*, and *Poliocitellus*; seven or eight in *Callospermophilus*; eight in *Cynomys*, *Marmota*, *Neotamias*, *Sciurus*, and *Tamiasciurus*; eight or nine in *Xerospermophilus* and *Ammospermophilus*; nine in *Glaucmys*; probably specifically variable in all forms.

Rhomboideus.—Synonym: rhomboideus anticus and posticus, Peterka, 1936. Other references to this muscle in sciurids refer at the same time to the occipitoscapularis, and a separation of the names applied to these two muscles is impossible. The following apply to both the rhomboideus and occipitoscapularis: rhomboideus major and minor, Hoffmann and Weyenbergh, 1870; rhomboideus capitis major and minor, Parsons, 1894; rhomboide de la tête et rhomboide du dos, Alezais, 1900.

Single; thin at origin and thick at insertion; ventral border in close contact with or inseparable from occipitoscapularis. Arises from middorsal part of superior nuchal line or from spine of axis, nuchal ligament, and supraspinous ligament of first four or five thoracic vertebrae; situated internal to trapezius; fibers converge toward scapula; inserts on entire vertebral border of scapula and on dorsal margin of subscapularis muscle except at caudal angle. Clearly separable from occipitoscapularis in *Xerospermophilus*, *Ammospermophilus*, *Neotamias*, and *Glaucmys*. Larger in *Marmota*. In tree and flying squirrels, which lack a definite cranial angle on scapula, insertion terminates cranially near dorsal tip of cranial subscapular ridge.

Occipitoscapularis.—Synonyms: see rhomboideus. Relations to rhomboideus discussed in preceding paragraph. Covers side of neck internal to acromiotrapezius and ventral to rhomboideus. Originates on caudal border of superior nuchal line, deep to origin of cleido-occipitalis; runs caudad and slightly dorsad; inserts on lateral surface of vertebral border of scapula from spine to cranial angle, on dorsal one-fourth of crest of scapular spine, and on dorsocaudal surface of supraspinatus.

Atlantoscapularis dorsalis.—Synonym: faisceau altoldien du rhomboide, Alezais, 1900. Arises on cranioventral surface of atlas, cranial to origin of scalenus; runs caudo-dorsolaterad across shoulder and side of neck in contact with atlantoscapularis ventralis to point caudal to tympanic bulla; internal to occipitoscapularis near insertion; inserts by fascia on cranial surface of scapular spine between supraspinatus and ventral part of occipitoscapularis. Absent in *Ictidomys*, *Xerospermophilus*, *Poliocitellus*, and subgenus *Citellus*. In *Cynomys* inserts in angle between scapular spine and cranial part of vertebral border.

Atlantoscapularis ventralis.—Synonyms: acromiobasilaris, Hoffmann and Weyenbergh, 1870; levator claviculae, Parsons, 1894; omo-transversaire, Alezais, 1900; omocervicalis, Hill, 1937. Arises on ventral surface of ventral arch of atlas lateral to attachment of longus colli and medial to attachment of scalenus; runs caudad and slightly laterad internal to occipitoscapularis and ventral to acromiotrapezius; inserts on caudo-ventral angle of metacromion.

LATISSIMUS-SUBSCAPULAR GROUP

Supplied by subscapular nerves

Latissimus dorsi.—Synonym: grand dorsal, Alezais, 1900. Originates on tips of spinous processes of last five or six thoracic and first or first two lumbar vertebrae, on lumbodorsal fascia, and by slips from last three ribs; fibers converge toward axilla internal to cutaneous maximus and spinotrapezius; in axilla merges and inserts with cutaneous maximus (see page 327). Slips arise from last four ribs in subgenus *Citellus*, *Poliocitellus*, *Cynomys*, and sometimes in *Ictidomys*, and from last five ribs in *Marmota*. Slips arise from twelfth or eleventh and twelfth ribs in *Neotamias*, *Sciurus*, *Tamiasciurus*, and *Glaucmys*.

Teres major.—Synonym: grand rond, Alezais, 1900. Arises on expansion below caudal angle of scapula, on crest of axillary ridge to level of infraglenoid fossa, and on fascia separating it from subscapularis; runs to axilla in close association with cranial

border of latissimus dorsi; inserts in common with latissimus dorsi on medial ridge of humerus shortly distal to lesser tuberosity; a low crest or rugosity marks place of insertion. Connection with latissimus dorsi more extensive in *Poliocitellus*, *Marmota*, *Sciurus*, and *Tamiasciurus*. Originates in large fossa in tree squirrels and in small fossa in chipmunks and flying squirrels. Much heavier in tree squirrels than in other sciurids. Inserts by special tendon partly proximal and partly caudal to insertion of latissimus dorsi in *Glaucomys*.

Subscapularis.—Divisible into four bipennate parts: one situated between caudal subscapular ridge and axillary border, one between the two subscapular ridges, and two smaller parts are present between cranial border and cranial subscapular ridge. Originates by sheath from axillary border, from subscapular fossa except the vertebral margin, and on fascia of teres major and supraspinatus; parts converge to common tendon in area medial to neck of scapula; inserts on capsule of shoulder joint and on lesser tuberosity. The two cranial parts meet along a low ridge in *Marmota*. Caudal part much shorter in *Sciurus*, *Tamiasciurus*, *Neotamias*, and *Glaucomys*, owing to larger area occupied by teres major. The higher cranial subscapular ridge extending nearly to cranial angle of scapula indicates a correlative increase in strength of bipennate part between cranial and caudal subscapular ridges. Only one bipennate part is present in front of cranial subscapular ridge in *Sciurus* and *Tamiasciurus*.

DELTOID GROUP. Supplied by axillary nerve.

Deltoideus. Divisible into clavoacromial and spinal parts; former further divisible into clavodeltoideus and acromiodeltoideus.

Clavodeltoideus.—Inseparably fused with acromiodeltoideus and closely associated with ectopectoralis. Composed of superficial and deep layers. Superficial layer arises opposite lateral part of origin of cleido-occipitalis on caudoventral surface of clavicle, except sternal one-fourth and scapular one-eighth; runs across craniomedial surface of shoulder and forearm; inserts by tendon in conjunction with brachialis on brachial ridge of ulna; this layer may be called clavobrachialis. Deep layer arises on clavicle dorsal to origin of clavobrachialis and is completely obscured by it; fibers converge to insert on deltoid process and slightly distal thereto; stouter than clavobrachialis. Superficial layer inserts on deltoid process distal to insertion of deep layer in *Ammospermophilus*, *Neotamias*, *Sciurus*, *Tamiasciurus*, and *Glaucomys*; not specialized as a clavobrachialis. Clavobrachialis heavier than deep layer in *Marmota*.

Acromiodeltoideus.—Originates by tendon on acromial tuberosity and on ventral margin of acromion cranial and caudal to tuberosity; fibers run obliquely mediolateral to join those of clavodeltoideus in a tendinous inscription; inserts on greater tubercle and crest of deltoid ridge. Acromial and clavicular parts cannot be distinguished in *Glaucomys*; deltoid ridge and insertion of clavoacromiodeltoideus relatively shorter. A few fibers attach to scapular tip of clavicle in *Neotamias*, *Marmota*, and *Glaucomys*. Origin on acromial tuberosity situated nearer tip of acromion in *Sciurus* and *Tamiasciurus*.

Spinodeltoideus.—Clearly separable from other parts of deltoideus. Arises on ventral three-fourths of caudal surface of crest of scapular spine, fascia of infraspinatus, and caudomedial margin of metacromion; inserts by long tendon on lateral margin of deltoid ridge approximately midway between proximal epiphyseal line of humerus and deltoid process. Origin extends to dorsal end of scapular spine in *Glaucomys*.

Teres minor.—Synonym: petit rond, Alezais, 1900. Arises by tendinous sheath on ventral half of axillary border of scapula, on sheath of infraspinatus, and on tendon of triceps brachii longus; runs external to infraglenoid tuberosity and caudal to ventral part of infraspinatus; inserts by tendinous sheath along epiphyseal line of head of humerus caudodistal to infraspinatus fossa; larger at insertion than at origin.

SUPRASCAPULAR GROUP. Supplied by suprascapular nerve.

Infraspinatus.—Arises by tendinous sheath from infraspinous fossa, on caudal surface of scapular spine below origin of spinodeltoideus, and on medial surface of metacromion;

inserts by strong tendon in infraspinatus fossa on lateral surface of greater tubercle of humerus. Narrower and thicker in *Neotamias*, *Sciurus*, and *Tamiasciurus*, in correlation with more nearly vertical direction of axillary ridge; narrower in *Glaucomys*.

Supraspinatus.—Arises from supraspinous fossa, fascia of subscapularis, and cranial surface of scapular spine; fibers converge ventrally and pass between acromion and neck of scapula; inserts by strong tendon on cranial surface of greater tubercle and proximal end of deltoid ridge. The slightly greater cranial inclination of the scapular spine in tree squirrels may be due to greater strength of this muscle.

TRICEPS GROUP. Supplied by radial nerve.

Triceps brachii.—Synonym: extensor brachii, Hoffmann and Weyenbergh, 1870. Situated on caudal surface of upper arm internal to dorsoepitrochlearis. Divided into three parts. Caput longum arises by flat tendon from infraglenoid fossa and tuberosity and by fibers from axillary border of scapula dorsal to fossa; origin internal to teres minor; largest head. Caput mediale (vaste interne, Alezais, 1900) has two divisions: one arises in notch between head and lesser tubercle of humerus, and other arises on caudomedial surface of proximal half of humerus and on caudal surface of distal half; completely separated from other heads of triceps but not clearly separable from anconeus near insertion; inserts on proximolateral surface of olecranon. Caput laterale (vaste externe, Alezais, 1900) about size of caput mediale; arises by tendon on proximal part of lateral border of humerus and on proximolateral edge of deltoid ridge distal to insertion of teres minor; unites with caput longum and inserts by strong tendon on lateral side of olecranon and by fascia on tricipital ridge of ulna. Proximal division of caput mediale relatively much larger in *Neotamias*, *Sciurus*, and *Tamiasciurus*. A small slip passes between caput mediale and caput longum in tree squirrels and marmos. Caput longum and caput laterale relatively weaker in *Glaucomys*.

Anconeus.—Synonym: anconeus lateralis, Peterka, 1937; also see epitrochleoanconeus (page 328). Not completely separated from caput mediale of triceps. Arises on caudal surface of lateral condyle and epicondylar ridge of humerus; runs distomedially; inserts on lateral surface of olecranon from near proximal end to level of semilunar notch.

Dorsoepitrochlearis.—Synonyms: fourth head extensor brachii, Hoffmann and Weyenbergh, 1870; dorso-olécrânien, Alezais, 1900; epitrochlearis, Peterka, 1937; tensor fasciae antibrachii, Bohmann, 1939. On caudal surface of upper arm superficial to other muscles. Arises from fascia on caudal border of teres major, near junction of teres major and latissimus dorsi, and on lateral border of infraglenoid fossa in close association with caput longum of triceps; inserts by sheath on medial surface of caput longum or is loosely attached to caput longum by fascia and inserts in general fascia of elbow joint. In ground squirrels, other than *Otospermophilus* and subgenus *Citellus*, and in marmos, tree squirrels and flying squirrels, it also attaches by fibers to latissimus dorsi. Stouter in tree squirrels and marmos. In *Glaucomys* it is a thin, band-like muscle with a limited origin on teres major at middle of axillary border of scapula.

EXTENSOR GROUP OF FOREARM. Supplied by radial nerve.

Brachioradialis.—Synonyms: supinator longus, Parsons, 1894, Peterka, 1937; long supinateur, Alezais, 1900. Arises on cranial surface of proximal half of lateral epicondylar ridge of humerus, opposite origin of anconeus and proximal to origin of extensor carpi longus; runs distad external to extensor carpi radialis longus and medial to extensor carpi radialis brevis; inserts by short and stout tendon on tubercle, which is located on outside of distal end of radius and is separated from styloid process by groove for tendon of abductor pollicis longus. In *Glaucomys* tendon at insertion is almost as long as body and is closely applied to distal one-third of radius.

Extensor carpi radialis longus.—Synonym: radialis externus longus, Hoffmann and Weyenbergh, 1870. Arises on lateral epicondylar ridge, distal to origin of brachioradialis and proximal to origin of extensor carpi radialis brevis; runs on cranial surface of forearm internal to brachioradialis and medial to brevis; tendon begins well proximal to distal

end of radius, passes over cranial surface of styloid process of radius parallel to tendon of brevis and internal to tendon of abductor pollicis longus; inserts in a small oblique groove, which is situated on radial margin of cranial surface of proximal end of second metatarsal. In one specimen the tendons of longus and brevis crossed, the former inserting on the third and the latter on the second metatarsal.

Extensor carpi radialis brevis.—Synonym: *radialis extensor brevis*, Hoffmann and Weyenbergh, 1870. Has short origin on crest of lateral epicondylar ridge of humerus proximal to lateral condyle but arises principally from craniodistal surface of ridge and from lateral border of coronoid fossa; runs distad on craniolateral surface of forearm craniomedial to extensor digitorum communis; long tendon passes in groove on radial side of styloid process of radius internal to tendon of abductor pollicis longus; inserts near proximal end of radial surface of third metacarpal.

Supinator.—Synonyms: *supinator brevis*, Parsons, 1894; *court supinateur*, Alezais, 1900. Arises by short tendon from radial collateral ligament and from distal edge of lateral epicondyle of humerus; fibers run distomedial on cranial surface of proximal end of radius; inserts by fascia on cranial border of radius from head to point past middle.

Abductor pollicis longus.—Synonyms: *extensor ossis metacarpi pollicis*, Parsons 1894; *extenseur du pouce*, Alezais, 1900; *extensor metacarpi pollicis*, Peterka, 1937. Arises by two short heads: smaller one by short tendon from lateral surface of radius distal to head, and larger by fascia from proximal end of lateral fossa of ulna; body attaches on oblique ridge and ulnar side of radius, on interosseous membrane, and on lateral fossa of ulna except the part occupied by extensor indicis. Tendon runs distomedial on cranial surface of distal end of radius and through radial compartment of wrist external to tendons of extensores carpi radiales. One division of the tendon inserts on proximal tip of falciform; the other division inserts on abductor process at proximolateral margin of first metacarpal. Small head to radius absent in *Marmota* and subgenus *Citellus*. Two heads separated for a greater distance in *Glaucomys* than in other sciurids. No tendon to falciform in *Sciurus*, *Tamiasciurus*, and *Glaucomys*.

The relations described above are constant in the forms examined but differ from findings of other workers. Hoffmann and Weyenbergh (1870) and Parsons (1894) found no origin on the radius in *Sciurus vulgaris* and *prevosti*, *Citellus mexicanus*, and *Marmota marmota*; Alezais (1900) states that this origin is present in *Sciurus vulgaris* but not in *Marmota marmota*. Peterka (1937) found the radial origin in *Sciurus niger*, *Cynomys ludovicianus*, and *Glaucomys volans*. The radial origin is also present in *Sciurus vulgaris* and *Marmota marmota* (Bohmann, 1939), in *Sciurus griseus* and *Citellus richardsonii* (Hill, 1937), and in *Citellus armatus* (Brizzee, MS). The presence or absence of a tendon to the falciform is variously reported in the several genera concerned.

Extensor digitorum communis.—Arises by tendon from rugosity on lateral epicondyle of humerus in contact with extensor digiti quinti proprius; runs along cranial surface of forearm; usually composed of two bipennate parts, each of which ends in two tendons proximal to wrist; tendons pass through middle compartment of wrist and diverge to ulnar side of base of second digit and radial sides of bases of third, fourth, and fifth digits; tendons run on dorsum of second through fifth digits, to which they are attached by fascia, and insert on dorsal surfaces of ungual phalanges proximal to claws. Slips terminating in tendons to second and fifth digits usually longer than those to third and fourth digits. Tendon to fifth digit absent in one specimen of *Sciurus niger*. Tendons broader in tree squirrels and longer in flying squirrels. The number of slips comprising the muscle and the relations of the tendons to the slips are individually variable.

Extensor indicis.—Synonym: *indicator*, Hoffmann and Weyenbergh, 1870. Arises on cranial surface of ulna distal and caudal to lateral fossa; small tendon passes through middle compartment of wrist and over third metacarpal to ulnar side of second digit; inserts on dorsum of first and second phalanges and on tendon of extensor digitorum communis of second digit. Origin more restricted in tree squirrels. Smaller in flying squirrels; arises along line of fusion of radius and ulna.

Extensor digiti quinti proprius.—Synonym: *extensor digiti minimi*, Hoffmann and Weyenbergh, 1870, Parsons, 1894. Inseparable from *extensor digitorum communis* at origin on lateral epicondyle of humerus; runs parallel to cranio lateral surface of ulna. Composed of two parts, from each of which a tendon arises proximal to wrist; tendon of radial part passes through medial compartment of wrist with tendons of *extensor digitorum communis* and inserts on proximal end of second phalanx of third digit (*extensor digiti tertii*, Bohmann, 1939); tendon of ulnar slip divides and passes through special compartment located between middle compartment and styloid process of ulna and inserts on ulnar sides of ungual phalanges of fourth and fifth digits (*extensores digiti quarti* and *minimi*, Bohmann, 1939). There is no special compartment for tendons to fourth and fifth digits in *Sciurus*, *Tamiasciurus*, and *Glaucomys*. In one specimen of *Cynomys* the tendon to third digit was absent.

Extensor carpi ulnaris.—Synonym: *cubital postérieur*, Alezais, 1900. Arises by short tendon in depression on distal surface of lateral condyle of humerus caudodistal to origin of *extensor digitorum communis* and by fascia from lateral ridge of ulna; tendon begins at distal end of ulna and passes through ulnar compartment on lateral surface of styloid process of ulna; inserts on tip of projecting lateral part of proximal end of fifth metacarpal. Origin on lateral condyle longer in tree squirrels.

FLEXOR SYSTEM

PECTORAL GROUP. Supplied by the two anterior thoracic nerves, except the subclavius which is supplied by a special branch from the brachial plexus.

The descriptions of the attachments of the parts of the pectoral muscle in sciurids vary widely; but, if one considers the muscle as a whole, the differences are slight. This results from varying interpretations of the limits of poorly defined divisions of the muscle. Furthermore, the insertions on the humerus and shoulder capsule are mostly aponeurotic and, in some instances, the limits of the insertions are purely arbitrary.

Ectopectoralis (pectoralis major).—Synonyms: alpha and beta parts of *pectoralis*, Parsons, 1894; *couche superficielle* et *couche moyenne* de *pectoralis*, Alezais, 1900; *pectoralis superficialis*, Peterka, 1937. Clearly separable from *pectoralis minor* except near caudal border. Arises from ventral surface of expanded cranial part of manubrium sterni and below origin of sternomastoideus slightly cranial thereto, from crest of manubrium, and from ventral surfaces of first four sternebrae; caudal fibers arise on ventral surfaces of sternal ends of costal cartilages of last two true ribs and on xiphisternal bone in union with *pectoralis minor*. Part arising from manubrium sterni much heavier than remainder of muscle but differentiated from remainder only in that the fibers run more obliquely. Fibers converge toward deltoid ridge. Inserts in a thin sheet on medial surface of deltoid ridge by fibers and on distal end of ridge by tendon. In *Sciurus*, *Tamiasciurus*, and *Neotamias* incompletely divided into three parts; in first two genera *ectopectoralis* extends to cranial tip of pointed manubrium sterni, in *Neotamias* some fibers arise from sternal end of clavicle. In *Glaucomys* arises from cranial surface of Y-shaped manubrium sterni, sternal end of clavicle, and by fascia from sternal ends of all costal cartilages that attach to the sternum except the third and fourth; insertion relatively shorter than in other sciurids in correlation with small size of deltoid ridge.

Entopectoralis.—Composed of four parts: *pectoralis minor*, *pectoralis abdominalis*, *entopectoralis profundus*, and *cutaneous maximus*.

Pectoralis minor.—Synonyms: delta part of *pectoralis*, Parsons, 1894; *pectoralis profundus*, Alezais, 1900, Peterka, 1937. Arises from ventrolateral surfaces of first four sternebrae and sternal ends of third through sixth or seventh costal cartilages; for origin in conjunction with *ectopectoralis* see discussion of *ectopectoralis*. Fibers run cranio-laterad, internal to *ectopectoralis*, with little convergence. Inserts on capsule of shoulder joint, craniomedial surface of lesser tubercle, and on oblique line from lesser tubercle to distal end of deltoid ridge slightly caudal to insertion of *ectopectoralis*. A fascial connection with coracoid process is occasionally present. In *Sciurus* and *Tamiasciurus* *pectoralis minor* arises, in addition to the points of origin in *Otospermophilus*, from

fifth sternebra, which is usually absent in other sciurids. Smaller in *Glaucomyss* than in other squirrels; arises from sternal ends of third and fourth costal cartilages and has more restricted insertion.

Pectoralis abdominalis.—Synonyms: gamma part of pectoralis, Parsons, 1894; xiphohumeralis, Brizzee, MS. Arises from xipisternal cartilage, midline of abdomen for short distance caudal to xiphisternum, and on adjacent abdominal fascia. Separated from remainder of pectoralis except near insertion; superficially situated from origin to level of fourth rib, where it passes internal to pectoralis minor; continuous with ventral margin of cutaneous maximus in axilla. Inserts with pectoralis minor by fascia on capsule of shoulder joint, craniomedial margin of lesser tubercle, and in area between deltoid ridge and lesser tubercle.

Entopectoralis profundus.—Synonym: sternocostalis, Hill, 1937. Arises by aponeurosis from second to fourth sternebrae and from sternal ends of third through fifth costal cartilages; runs craniolaterad on ventral surface of rectus abdominis, its fibers beginning near the lateral margin of this muscle; attaches to caudoventral surface of first rib at junction of cartilage and bone lateral to attachment of subclavius and caudal to origin of ventral part of scalenus. Absent in *Glaucomyss*.

This muscle appears to have been overlooked by many investigators. I have accepted Lander's (1918) interpretation of its relationships. The sterno-costal, figured but not discussed by Alezais (1900, fig. xli) in *Sciurus vulgaris*, seems to be this muscle. It is described by Langworthy (1924) as the fourth pectoral layer in the cat and dog.

Cutaneous maximus.—Synonyms: panniculus carnosus (part), Parsons, 1894; pannicle charnu proprement dit, Alezais, 1900. Composed of humeral and ventral divisions. Humeral part inserts by two slips; one on distal part of fascia of insertion of pectoralis minor, and the other in close association with proximal end of latissimus dorsi on fascia at contact of triceps brachii and teres major. A tendon at cranial margin of fascia attaches both slips to a low process on medial ridge of humerus shortly distal to lesser tubercle; slips come together in axilla and fibers spread dorsad to interscapular area, dorsocaudad to sides and top of chest and abdomen, and nearly caudad to thigh; fibers of right and left sides form continuous sheet in middorsal line; fibers converge dorsal to cranial end of ilium to form a strong band that attaches near fourth caudal vertebra. Ventral divisions closely connected to pectoralis abdominalis at and near insertion; fibers run caudad lateral to linea alba and in contact with humeral division from axilla nearly to groin, where they continue as a definite slip to perineal region; no fibers on ventral part of breast or midventral line of abdomen. Dorsal part heavier in *Cynomys* and *Marmota*.

Cutaneous maximus highly specialized in *Glaucomyss*. No dorsal fibers to tail. A band composed of fibers of both humeral and ventral divisions runs parallel to upper arm from axilla past level of elbow and bends caudad. Fibers spread out over side of body from elbow to knee, converge to form a narrow band running cranial and parallel to leg, and attach to cranial surface of skin of ankle. Other fibers arise caudad to wrist and run along cartilage of membrane to join longitudinal band caudad to elbow; fibers also arise from palmar surface of wrist and attach to styloform cartilage and longitudinal band. Transverse fibers of indeterminate relations occur on side of trunk. The cutaneous maximus pulls the membrane laterad to a line between the wrist and ankle when it contracts; the transverse fibers probably hold the membrane next to the body when the membrane is not in use.

Subclavius.—Arises on cranial surface of first costal cartilage, usually near sternal end; runs craniolaterad; inserts on dorsal margin of scapular two-thirds of clavicle.

FLEXOR GROUP OF ARM. Supplied by musculocutaneous nerve, except for some fibers of brachialis which are supplied by radial nerve.

Coracobrachialis.—Arises on tip of coracoid process of scapula by two heads. Tendon of long part of muscle continues from origin to insertion; long part runs distad medial to insertions of subscapularis and latissimus dorsi; inserts by fascia on medial ridge,

on medial surface of shaft, and on medial epicondylar ridge of humerus; terminates within epicondylar foramen or in this area when foramen is absent. Short part of muscle arises on deep surface of tendon of long part near origin; inserts on proximal end of medial ridge, distal to proximal epiphyseal line of humerus between insertions of subscapularis and teres major. In *Glaucomys* short part not appreciably broader than long part, and has separate origin on inner surface of coracoid process; tendon of long part not continuous through muscle.

Biceps brachii.—Synonym: biceps cubiti, Parsons, 1894. Caput longum arises by long tendon from supraglenoid tuberosity; tendon runs on cranial surface of shoulder in intertubercular sulcus; fibers begin deep to ectopectoralis; muscle passes cranial to elbow and inserts by strong tendon to process on ulnar side of radius slightly distal to coronoid process of ulna. Caput breve present in one of four specimens; separates from cranial surface of caput longum and attaches to medial surface of coracobrachialis at level of distal end of deltoid ridge. Caput breve present in subgenus *Citellus*, *Ammodontomys*, *Cynomys*, *Marmota*, *Neotamias*, *Sciurus*, *Tamiasciurus*, and *Glaucomys*; attaches to coracobrachialis from near shoulder nearly to elbow; attachment to caput longum variable but usually at level of elbow. A slip of caput breve joins fascia of pronator teres in *Marmota*, *Sciurus*, and *Tamiasciurus*. Bohmann (1939) considers the slip here called caput breve as a part of coracobrachialis.

Brachialis.—Synonyms: brachialis internus, Hoffmann and Weyenbergh, 1870; brachialis anticus, Parsons, 1894. Has two incompletely separated heads. Superficial head arises by tendon caudal and lateral surfaces of proximal end of humerus distal to insertion of caput laterale of triceps brachii and by fibers from lateral surface of deltoid ridge; twists medially around humerus as it runs distad. Deep part arises on cranial and lateral surfaces of shaft of humerus distal to deltoid ridge; joins superficial part in coronoid fossa of humerus; both parts insert by flat tendon on proximal part of tuberosity of ulna and on cranial surface of coronoid process. Superficial and deep layers not clearly discernible in subgenus *Citellus* and *Ictidomys*.

FLEXOR GROUP OF FOREARM. Supplied by median and ulnar nerves.

Epitrochleo-anconeus.—Synonyms: epitrochléo-olécranien, Alezais, 1900; anconeus, Peterka, 1937, Bohmann, 1939. Situated on medial surface of elbow. Arises on caudal surface of medial epicondyle of humerus; inserts on medial surface of olecranon in notch near proximal end; difficult to separate from flexor carpi ulnaris near insertion.

Flexor carpi ulnaris.—Synonym: cubital antérieur, Alezais, 1900. Arises by two heads. One head arises from depression in medial surface of olecranon process and on caudal surface of proximal end; tendon forms on medial border of muscle; outer fibers run caudomedially; fibers end shortly proximal to wrist and strong tendon continues caudal to styloid process of ulna; inserts on distal tip of pisiform. Second head arises by tendon from caudal surface of medial epicondyle of humerus in common with origins of epitrochleo-anconeus and palmaris longus. In *Glaucomys* the tendon becomes larger near insertion and attaches to middle of proximal end of styloid cartilage of membrane as well as to pisiform; muscle pulls cartilage in toward arm and folds membrane.

Palmaris longus.—Arises on distal margin of medial epicondyle of humerus by long tendon, which runs deep to proximal ends of flexor carpi ulnaris and flexor digitorum profundus; situated on caudal surface of forearm; fibers end in broad tendon proximal to wrist; inserts broadly in palmar fascia at bases of thenar and hypothenar pads; a special tendon to thenar or to hypothenar or to both pads may be present. Smaller in *Glaucomys* and tendon at insertion more distinct than in other sciurids.

Flexor carpi radialis.—Synonym: grand palmaire, Alezais, 1900. Arises on medial epicondyle of humerus in common with condyloradial head of flexor digitorum communis; body passes into tendon proximal to wrist; tendon runs along radius and internal to falciform through notch in semilunar, deep to carpal-metacarpal ligament; inserts by fascia on base of second metacarpal and by tendon to radial side of proximal end of third metacarpal; closely attached to proximolateral end of first metacarpal by fascia;

attachment to third metacarpal stronger than other attachments. A definite tendon inserts on first metacarpal in *Sciurus* and *Neotamias*. Some investigators state that the insertion of this muscle is limited to second metacarpal. This was not true in any of the specimens examined in this study.

Pronator teres.—Synonyms: pronator radii teres, Parsons, 1894; rond pronateur, Alezais, 1900. Arises by tendon from medial end of medial epicondyle of humerus; runs obliquely distolaterad; inserts by broad, flat tendon on medial ridge of middle third of radius, medial to insertion of supinator. Insertion nearer proximal end of radius in *Glaucomys*.

Flexor digitorum sublimis.—Synonym: fléchisseur perforé, Alezais, 1900. Arises on caudal surface of medial epicondyle of humerus in notch medial to trochlea and on tendon of palmaris longus. Composed of four closely united bipennate bodies, which end in long tendons that go to second through fifth digits; tendons run in groove formed by palmar radiocarpal ligament, pisiform, and falciform and then pass to palmar surfaces of second through fifth digits. Each tendon splits below metacarpophalangeal joint, and tendon of flexor digitorum profundus passes through opening; the two parts of tendon reunite slightly proximal to distal end of first phalanx; a small tendon arises from each side of main tendon and inserts on processes on proximal end of palmar surface of second phalanx; main tendon held tightly to phalanges by ligaments.

Flexor digitorum profundus.—Synonym: fléchisseur perforant, Alezais, 1900. Composed of four distinct heads situated along caudal surfaces of radius and ulna. Ulnar head large; arises on medial surface of ulna from point slightly distal to tuberosity nearly to wrist. Central head smallest; arises by tendon from notch on caudal surface of medial epicondyle of humerus. Condyloradial head about the same size as ulnar head; arises on distal end and craniodistal margin of medial epicondyle with flexor carpi ulnaris. Radial head approximately equal to ulnar head in size; arises deep to pronator teres on medial surface of radius from level of insertion of biceps brachii to flattened distal end of radius; radial and ulnar heads unite proximal to wrist. Tendon of radial and ulnar heads broad, deep to tendons of other heads; all tendons fuse below carpus, except a branch from tendon of condyloradial head that inserts on tubercle on palmar surface of ungual phalanx of pollex; broad and flat common tendon then divides into four tendons that insert on second through fifth ungual phalanges. Relations of the four tendons to those of flexor digitorum sublimis discussed in preceding paragraph. Although a tendon to the pollex was present in all of the specimens I examined, it has been reported absent in *Sciurus* and *Marmota* (Parsons, 1894, and Alezais, 1900).

Pronator quadratus.—Synonym: carré pronateur, Alezais, 1900. Flat muscle with transverse fibers. Arises from fossa on radial surface of distal one-third of ulna; inserts on flattened ulnar surface of distal two-fifths of radius. Exhibits wide individual variation in size. No evidence of this muscle was found on proximal half of forearm (see Peterka, 1937).

FLEXOR GROUP OF MANUS

Abductor pollicis brevis.—Synonym: flexor pollicis brevis, Hoffmann and Weyenbergh, 1870, Peterka, 1937. Arises on dorsal surface of base of falciform and major multangular; runs distad; inserts on sesamoid bones at proximal end of first phalanx of pollex, but principally on radial one. In *Glaucomys* composed of a few fibers arising from distal border of falciform.

Abductor pollicis.—Arises on carpal ligament and on radial edge of centrale distal to radial margin of scapholunar; runs distomedial; inserts on ulnar surface of first phalanx of pollex, distal to ulnar sesamoid.

Abductor digiti quinti.—Arises by fascia from tip of pisiform distal to insertion of flexor carpi ulnaris; runs distad and slightly laterad; inserts by fascia on ulnar sesamoid at proximal end of first phalanx of fifth digit. Inserts by tendon almost as long as body in *Ammospermophilus*, *Cynomys*, and *Neotamias* and by longer tendon in *Glaucomys*. Origin in *Sciurus* and *Tamiasciurus* as in *Otospermophilus*, but muscle joins flexor digiti quinti brevis shortly before its insertion and the two insert by a common broad tendon.

Opponens digiti quinti.—Synonym: flexor digiti quinti, Hoffmann and Weyenbergh, 1870. Arises on proximoventral surface of hamate and adjacent carpal ligament below origin of fourth interosseous muscle; runs distolaterad below fifth and sixth interossei; inserts on radial sesamoid at proximal end of first phalanx of fifth digit. Appears heavier in tree squirrels.

Flexor digiti quinti brevis.—Synonyms: abductor digiti quinti (part), Hoffmann and Weyenbergh, 1870; flexor brevis manus, Parsons, 1894. Arises by fascia on dorsal side of distal tip of falciform; runs laterad and slightly distad ventral to tendons of flexor digitorum profundus; inserts with abductor digiti quinti by fascia on ulnar sesamoid of proximal phalanx of fifth digit. In *Ammospermophilus* and *Neotamias* arises partly from cartilage of hypothenar pad and inserts by tendon. Arises by short tendon in *Cynomys* and inserts broadly on tendon of flexor digitorum sublimis to fifth digit in area dorsal to proximal end of fourth metatarsal. In *Sciurus* and *Tamiasciurus* arises more on proximomedial border of cartilage of hypothenar pad than on falciform; joins abductor digiti quinti shortly before insertion and inserts with it by common tendon.

Palmaris brevis.—Imbedded in connective tissue of thenar and hypothenar pads. One part arises on dorsal surface of falciform and on skin of ulnar side of pollex; inserts in thenar and hypothenar pads. Second part arises in skin at fifth metatarsophalangeal joint; inserts in hypothenar pad. Absent (?) in *Neotamias*, *Sciurus*, and *Tamiasciurus*. In *Glaucomys* a ligament, which may be a remnant of this muscle, extends from dorsal surface of falciform to laterodistal tip of styloform cartilage.

Lumbricales.—Four; arise from palmar surface of body of tendon of flexor digitorum profundus near distal margin; run between tendons of deep flexor that go to digits; insert on radial sides of first phalanges of second through fifth digits slightly distal to radial sesamoids.

Interossei.—Eight; arise on palmar surface of distal row of carpals and on second through fifth metacarpals; insert by short tendons on proximodorsal margins of sesamoid bones of second through fifth metacarpophalangeal joints. Situated deep to tendons of flexor digitorum profundus. First and second interossei arise deep to origin of abductor pollicis; third, fourth, fifth, and sixth interossei arise deep to origin of opponens digiti quinti; seventh and eighth interossei arise distal to base of pisiform.

MUSCLES OF THE PELVIC GIRDLE AND LIMB EXTENSOR SYSTEM

ILIACUS GROUP. Supplied by branches of the femoral nerve except part of pectineus, which is supplied by obturator nerve.

Iliacus.—Separable into larger lumbar and smaller iliac parts. Iliac part arises from ventral part of inferior gluteal fossa ventral to origin of gluteus minimus and from ventral part of anterior superior iliac spine. Lumbar part arises from transverse processes of fifth through seventh lumbar vertebrae and ventral surface of sacrospinalis muscle; separated from psoas major by femoral nerve. The two parts unite at point cranial to anterior inferior iliac spine and insert by strong, flat tendon on cranial surface of lesser trochanter. Iliacus closely associated with psoas major at insertion. In *Sciurus* and *Tamiasciurus* iliac and lumbar parts more clearly separated; iliac part arises only on border of inferior gluteal fossa.

Psoas major.—Closely associated with lumbar part of iliacus, from which it is separated by femoral nerve. Arises from sides of bodies and ventral surfaces of transverse processes of last few lumbar vertebrae; inserts by tendon on tip of lesser trochanter and on capsule of hip. Lumbar part of iliacus sometimes considered as part of psoas major.

Pectineus.—Arises on ridge caudal to iliopectineal eminence craniodorsal to insertion of adductor longus; passes distad cranial to adductor longus, ventral to iliacus and psoas major, and caudal to vastus medialis; inserts on pectineal line distal and slightly

caudal to lesser trochanter of femur. In *Sciurus pectineus* is fused with adductor longus except at origin; other investigators have found them to be separate.

GLUTEAL GROUP. Supplied by superior and inferior gluteal nerves and common peroneal nerve. Composed of two layers; superficial layer comprises tensor fascia lata, gluteus maximus, femorococcygeus, and tenuissimus; deep layer composed of gluteus medius, gluteus minimus, and piriformis.

Tensor fascia lata.—Synonym: gluteus superficialis, Peterka, 1937. Arises by fascia from outer lip of iliac crest, gluteus medius, iliac ridge, inguinal ligament caudal to iliac crest, and lumbodorsal fascia above seventh lumbar and first sacral vertebrae; continuous with and inseparable from cranial border of gluteus maximus; fibers terminate lateral to gluteus medius. Caudal part inserts near middle of thigh on fascia external to vastus lateralis and on tendon of gluteus maximus; cranial part inserts on fascia lata on cranial border of vastus lateralis and is separated from origin of sartorius by a short space. In *Marmota* it does not arise from iliac crest cranial to superior gluteal fossa but has heavier attachment to anterior superior iliac spine. In *Glaucomys* completely separate from gluteus maximus; longer and thinner; arises only on anterior superior iliac spine and iliac ridge; inserts in fascia lata shortly proximal to knee, more distally than in other sciurids; no cranial and caudal divisions.

The part arising from inguinal ligament is, in some specimens, incompletely separated from remainder of muscle and appears as a separate slip. This slip has been called sartorius by Bohmann (1939: 368), but it lacks the typical relations of this muscle and is innervated by a branch of the superior gluteal nerve. This part is larger in *Sciurus* and *Tamiasciurus* than in other forms and is absent in *Glaucomys*.

Gluteus maximus.—Synonym: grand fessier, Alezais, 1900. Arises from lumbodorsal fascia above sacral vertebrae, on caudal margin of tensor fascia lata and on fascia of caudal part of gluteus medius. Some fibers connect to femorococcygeus. Inserts by strong tendon on gluteal tuberosity and on lateral ridge of femur for a short distance distal to tuberosity. In *Glaucomys* not fused with tensor fascia lata; arises from lumbodorsal fascia from level of seventh lumbar to level of first caudal vertebra and from iliac ridge; inserts on fascia lata lateral to proximal part of vastus lateralis and on small gluteal tuberosity.

Femorococcygeus.—Synonyms: superficial head of biceps femoris, Parsons, 1894; biceps femoris anticus, Peterka, 1937; biceps femoris I, Bohmann, 1939. Arises by short and broad tendon from fascia dorsal to first two caudal vertebrae and on lateral margins of transverse processes of these vertebrae. Some fibers unite with gluteus maximus. Proximal part runs dorsal to lesser sciatic notch, caudal to gluteus maximus, and cranial to biceps femoris. Inserts by short tendon on lateral surface of distal end of femur proximal to lateral condyle and on lateral ridge for a short distance proximally. Broader at origin in *Glaucomys*; arises on transverse processes of first four caudal vertebrae.

Tenuissimus.—Synonym: chef sacré du biceps fémoral, Alezais, 1900. Arises on transverse processes of third (or fourth) sacral and first caudal vertebrae, deep to caudal part of origin of gluteus maximus; runs deep to biceps femoris; inserts on fascia about two-thirds of distance from proximal end of leg, near distal margin of insertion of biceps femoris. Inserts near middle of leg in tree squirrels, chipmunks, and flying squirrels.

Gluteus medius.—Synonym: moyen fessier, Alezais, 1900. Arises from lumbodorsal fascia above seventh lumbar and first sacral vertebrae, fascia of extensor caudae lateralis, and in superior gluteal fossa; ventral part covers gluteus minimus and arises from iliac ridge by fascia. Inserts by short tendons on caudal margin of greater trochanter and on proximal end of greater trochanter in contact with and lateral to insertion of piriformis. Fibers arising in superior gluteal fossa sometimes separate from superficial fibers and insert by separate tendon in common with piriformis. In *Cynomys* there is no connection to iliac ridge and the origin on iliac spine is stouter. In tree squirrels,

chipmunks, and flying squirrels, the part that arises on iliac ridge in *Otospermophilus* arises slightly dorsal to the ventral border of the ilium. This results from relatively larger size of *gluteus minimus* and reduced size of inferior gluteal fossa in these forms.

Piriformis.—Arises from tips and ventral surfaces of transverse processes of last two (or three) sacral vertebrae and in depression on caudal surface of sacroiliac joint; passes through greater sciatic notch; inserts by short tendon on proximal end of greater trochanter of femur. In *Marmota* the origin does not extend to ventral surface of first sacral vertebra.

Gluteus minimus.—Synonym: petit fessier, Alezais, 1900. Dorsal part arises from iliac ridge, anterior superior iliac spine, dorsal part of inferior gluteal fossa, ilium dorsal to anterior superior iliac spine and acetabulum, and capsule of hip. Ventral part smaller than dorsal part; arises between caudoventral region of dorsal part and ventral part of *gluteus medius*; probably equivalent to *scansorius*; inserts partly on tendon of dorsal part and partly on proximal end of medial surface of greater trochanter. Dorsal part inserts by tendon on cranial part of greater trochanter. Ventral part relatively larger in tree and flying squirrels.

QUADRICEPS FEMORIS GROUP. Supplied by branches of femoral nerve.

Rectus femoris.—Synonyms: droit antérieur, Alezais, 1900. Arises by short and stout tendon from anterior superior iliac spine and craniodorsal margin of acetabulum; tendons united by heavy fascia and not clearly delimited; runs distad on cranial surface of thigh medial to *vastus lateralis* and cranial to *vastus medialis* and *vastus intermedius*; inserts by large tendon on cranial surface of patella and indirectly by patellar tendon tuberosity of tibia. The two tendons at origin are more clearly separated in *Sciurus*, *Tamiasciurus* and *Neotamias*.

Vastus lateralis.—Synonym: *vastus externus*, Hoffmann and Weyenbergh, 1870, Parsons, 1894, Alezais, 1900. Arises by short and broad tendon from cranial surface of greater trochanter except proximal tip, cranial surface of gluteal tuberosity, and from ridge between greater trochanter and gluteal tuberosity. Situated cranial and lateral to femur and lateral to *rectus femoris* and *vastus medialis*; proximal part covered by tensor fascia lata. Inserts by fascia on distal part of *rectus femoris* and proximal end of its insertional tendon, and on lateral side of patella and adjacent fascia.

Vastus medialis.—Synonym: *vastus internus*, Hoffmann and Weyenbergh, 1870, Alezais, 1900. Arises by fascia from cranial surface of neck of femur, capsule of hip, and proximal two-thirds of medial side of shaft of femur. Situated on craniomedial surface of femur, medial to *vasti intermedius* and *lateralis* and caudal to *rectus femoris*. Inserts on medial side of insertional tendon of *rectus femoris*, fascia medial to knee, and to a small extent on medial side of patella. In one specimen of *Neotamias* and one of *Marmota* inseparable from *vastus intermedius*.

Vastus intermedius.—Synonyms: *vastus medius*, Hoffmann and Weyenbergh, 1870; *crural*, Alezais, 1900. Arises from cranial surface of shaft of femur from level of gluteal tuberosity to distal end and on sides of shaft near distal end; runs deep to *vastus lateralis*; inserts on cranial end and sides of patella and by sheath of patella to tendon of *rectus femoris*. Arises farther distally in *Glaucomys*.

Crurales.—Two small muscles on medial and lateral sides of distal end of femur; deep to *vasti medialis* and *intermedius*, from which not always separable; run between condyles and ridges on sides of trochlea; insert on medial and lateral margins of patella.

Sartorius.—Synonyms: *couturier*, Alezais, 1900; *gracilis anticus*, Peterka, 1937; anterior portion of *gracilis*, Bohmann, 1939, Saccomanno, MS; cranial portion of *gracilis*, Brizzee, MS. Strap-like; very thin; varies greatly in width. Arises on inguinal ligament below *iliacus*, *pectineus*, and *adductor longus*, and cranial to origin of *gracilis*; no connection to *os coxae*; runs distad and slightly caudad on medial surface of thigh; inserts broadly by fascia on patella and medial surface of knee joint. Usually united

by fascia with distal end of gracilis but may fuse with it near insertion. Completely separated from gracilis in *Marmota*; more completely fused with gracilis in *Neotamias*, *Sciurus*, and *Tamiasciurus*; absent in *Glaucmys*.

This muscle is innervated by the saphenous branch of the femoral nerve and not, insofar as I could determine, by the superior gluteal nerve as stated by Parsons (1894: 282). The muscle in *Neotoma* called the anterior head of the gracilis by Howell (1926:79) and in *Rattus* called gracilis anticus by Greene (1935:54) arises from the pubis, deep to the origin of the adductor longus, and is supplied by the obturator nerve. It seems that the muscle in squirrels called the gracilis anticus (or its equivalent) is homologous to the sartorius of man, the origin having shifted from the ilium to the inguinal ligament, and that the gracilis anticus of myomorphs is appropriately named.

TIBIAL EXTENSOR GROUP. Supplied by deep peroneal nerve.

Extensor digitorum longus.—Synonyms: extensor digitorum pedis communis, Hoffmann and Weyenbergh, 1870; extenseur commun des orteils, Alezais, 1900; extensor digitorum communis, Bohmann, 1939. Arises by long tendon in small depression on craniolateral surface of lateral condyle of femur lateral to distal end of lateral patellar ridge; in contact with fibular collateral ligament. Runs distad on cranial surface of leg craniolateral to extensor hallucis longus, medial to peroneus longus, and caudal and lateral to tibialis anterior. Ends in four tendons at point one-fifth or less of length of tibia from distal end; tendons run internal to ligamentum transversum cruris and through loop arising on cranial surface of calcaneus; tendons diverge to bases of second through fifth digits; each tendon inserts on base of ungual phalanx and by fascia to other phalanges and to distal end of metatarsal. Small tendons interconnect the four tendons in some animals; these are individually variable. In *Citellus interpares* a tendon arises from proximal end of tendon to fifth digit, passes over tendons to third and fourth digits, and joins fascia at base of second digit. In *Sciurus niger* connections are present between tendons to second and third digits and tendons to fourth and fifth digits. The first of these connections is present in *Tamiasciurus douglasii*, and the latter is present in *Sciurus griseus*.

Extensor hallucis longus.—Synonyms: extensor proprius hallucis, Parsons, 1894; extenseur propre du gros orteil, Alezais, 1900; extensor hallucis, Peterka, 1937. Arises on cranial part of middle half of interosseus crest of fibula and corresponding length of interosseus membrane. Fibers end in tendon at level of tarsus; tendon runs deep to ligamentum transversum cruris and cruciatum cruris along with tendon of tibialis anterior and divides at level of middle of first metatarsal; one division inserts on ungual phalanx of hallux in same manner as tendons of extensor digitorum longus insert on other four digits; the other division inserts on proximomedial end of first phalanx of second digit or joins the extensor tendon to this digit. Tendon to second digit absent (?) in *Neotamias*, and *Glaucmys sabrinus*.

Tibialis anterior.—Synonyms: extensor tibialis anticus, Hoffmann and Weyenbergh, 1870; tibialis anticus, Parsons, 1894, Peterka, 1937; tibial antérieur, Alezais, 1900. Arises from cranial margin of lateral condyle, proximal half of lateral surface of tibia, and fascia of peroneus longus; small slip arises from cranial end of interosseus membrane and crest of fibula caudal to origin of peroneus longus; fibers end in stout tendon shortly proximal to tarsus; tendon runs distad and slightly mediad with tendon of extensor hallucis longus; inserts on medial surface of first cuneiform and adjacent surface of first metatarsal. Slip originating on fibula larger in *Glaucmys*.

PERONEAL GROUP. Supplied by common peroneal nerve. The muscles and tendons in this group in order of decreasing size are: peroneus brevis, peroneus longus, extensor digitorum brevis of fifth digit, extensor digitorum brevis of fourth digit, and extensores digitorum breves of third and second digits.

Peroneus longus.—Arises on lateral and cranial surfaces of head of fibula distal to attachment of fibular collateral ligament and lateral to small head of tibialis anterior; ends in tendon at point about one-sixth length of fibula from distal end. Tendon runs

through special osteofascial compartment caudal to lateral malleolus of fibula (most lateral of four peroneal tendons), lateral to body of calcaneus, through sulcus of cuboid to sole of foot, and mediad to insert on proximolateral tip of first metatarsal.

Peroneus brevis.—Arises by fleshy fibers from distal half of lateral surface of fibula, from cranial and lateral borders of fibula except at proximal and distal ends, and from fascia of extensores digitorum breves; ends in stout tendon shortly proximal to lateral malleolus of fibula. Tendon passes through compartment caudal to lateral malleolus in common with other peroneal tendons, runs in groove on cranial surface of trochlear process of calcaneus, and inserts on tuberosity at proximolateral tip of fifth metatarsal.

Extensor digitorum brevis of fifth digit.—Synonyms: peroneus brovis (part), Hoffmann and Weyenbergh, 1870; peroneus digiti quinti, Parsons, 1894, Peterka, 1937, Bohmann, 1939; péronier du cinquième doigt, Alezais, 1900. Arises by fascia on proximal half of lateral surface of fibula; proximal end attaches strongly to epiphyseal line of head lateral to attachment of small head of tibialis anterior and distal to origin of peroneus longus. Tendon begins at point two-thirds distance down fibula; runs parallel to tendon of peroneus brevis, through compartment caudal to lateral malleolus of fibula, and along dorsolateral margin of fifth metatarsal. Inserts on lateral side of distal end of fifth metatarsal and on first and proximal end of second phalanges of fifth digit.

Extensor digitorum brevis of fourth digit.—Synonyms: peroneus brevis (part), Hoffmann and Weyenbergh, 1870; peroneus digiti quarti, Parsons, 1894, Peterka, 1936, Bohmann, 1939; péronier du quatrième doigt, Alezais, 1900. Arises by fleshy fibers on lateral border and lateral surface of distal three-fifths of fibula medial to peroneus longus and extensor digitorum brevis of fifth digit. Tendon small; begins shortly proximal to lateral malleolus of fibula; runs through compartment caudal to lateral malleolus and to lateral side of base of fourth metatarsal. Inserts on lateral side of distal end of fourth metatarsal and first phalanx of fourth digit and on proximal end of second phalanx.

Extensores digitorum breves of third and second digits.—Synonyms: pédieux, Alezais, 1900; extensor digitorum brevis, Peterka, 1937. Arise by fascia from dorsal part of calcaneum medial to distal end of trochlear process and distal to talus; situated deep to tendon of extensor digitorum longus. Tendon of brevis of third digit runs to lateral side of base of third digit and inserts as do the breves of fourth and fifth digits. Tendon of short extensor of second digit divides; one branch inserts on second digit in same manner that other breves insert; other branch runs mediad below lateral tendon of extensor hallucis longus and inserts on base of first phalanx of hallux. Branch to hallux absent in *Marmota*, *Sciurus*, *Tamiasciurus*, *Neotamias*, and *Glaucomys*.

FLEXOR SYSTEM

ADDUCTOR GROUP. Innervated by obturator nerve.

Gracilis.—Synonyms: droit interne, Alezais, 1900; posterior portion of gracilis, Bohmann, 1939, Saccomanno, MS; caudal portion of gracilis, Brizzee, MS. Arises slightly lateral to midline on ventral surface of os coxae from ventral ischial tuberosity to pubic tubercle or on pubic ramus cranial to tubercle; runs distad on medial surface of thigh, caudal to sartorius and medial to semimembranosus; inserts on crest of tibia proximal to insertion of semitendinosus and distal to insertion of semimembranosus; usually unites with sartorius near distal end. More closely united to sartorius in *Neotamias*, *Sciurus*, and *Tamiasciurus*. Arises on ventral third of pubic ramus in *Glaucomys* in correlation with shortness of pubic symphysis.

There is only one part of the gracilis in sciurids. The reports of two divisions results from calling the sartorius, as here interpreted, a part of the gracilis.

Adductor longus.—Synonyms: pectineus (part), Hoffmann and Weyenbergh, 1870; adductor 1, Parsons, 1894; adducteur moyen, Alezais, 1900. Arises on cranial edge of cranial ramus of pubis shortly dorsolateral to pubic tubercle and between origins of

adductor brevis and pectineus; runs distal caudal to pectineus and cranial to adductor brevis; inserts by long tendon at distal end of spiral line of femur distal to insertion of pectineus and cranial to insertion of part of adductor brevis; fibers of adductor brevis attach to tendon. In *Glaucomyss* tendon is almost as long as body and inserts distal to pectineus. More closely fused with adductor brevis in *Sciurus* and *Tamiasciurus*.

Adductor brevis.—Synonym: portion antérieure et superficielle du grand adducteur, Alezais, 1900. Arises between origins of obturator externus and gracilis on pubis ventral to obturator foramen and on cranial ramus of pubis cranial to symphysis; usually in contact with caudal margin of adductor longus but may extend cranial internal to it. Runs distad along medial surface of femur cranial to adductor magnus and lateral to gracilis; cranial border touches adductor longus and pectineus. Inserts medial to insertions of distal part of adductor minimus and adductor magnus proprius on caudomedial border of femur from pectineal line to insertion of adductor magnus; some fibers attach to tendon of adductor longus. In *Glaucomyss* it arises on ventral ramus of pubis and on ventral one-half of dorsal ramus.

Adductor magnus.—Synonyms: adductor magnus (part), Hoffmann and Weyenbergh, 1870, Peterka, 1937; adductor 2, Parsons, 1894; portion postérieure et superficielle du grand adducteur, Alezais, 1900. Arises on os coxae cranioventral to ventral ischial tuberosity between origins of gracilis and adductor minimus and caudal to origin of adductor brevis. Parallel and closely adherent to medial border of adductor brevis. Inserts on distal end of caudomedial surface of femur in line with insertion of adductor brevis, on medial epicondyle, on ridge at proximal end of intercondylar notch, and on caudal surface of capsule of knee; contacts medial head of caudofemoralis at most distal point of insertion. Clearly separable from adductor brevis in *Marmota*, *Sciurus*, *Tamiasciurus*, and *Glaucomyss*; variable in other forms.

Adductor minimus.—Synonyms: adductor magnus (part), Hoffmann and Weyenbergh, 1870, Peterka, 1937; adductor 5, Parsons, 1894; petit adducteur, Alezais, 1900. Largest of adductors except adductor brevis. Arises on caudal two-thirds of horizontal ramus of pubis between origins of adductor brevis and obturator externus; runs nearly horizontally-cranial to caudofemoralis and caudal to adductor brevis; inserts on caudal surface of gluteal tuberosity and on lateral ridge proximal to origin of adductor magnus proprius and lateral to insertion of adductor brevis. Arises deep to origin of adductor magnus in *Glaucomyss* and on caudal part of shortened horizontal ramus of pubis.

Adductor magnus proprius.—Synonyms: adductor magnus (part), Hoffmann and Weyenbergh, 1870, Peterka, 1937; adductor 3, Parsons, 1894; portion tendineuse du grand adducteur, Alezais, 1900. Arises by short tendon on ischium between ventral part of ventral ischial tuberosity and obturator foramen dorsal to origin of adductor magnus and cranial to origin of ventral part of semimembranosus; runs distad lateral and caudal to adductor brevis, cranial to caudofemoralis, and medial to adductor minimus; inserts obliquely on medial epicondylar ridge of femur between insertions of adductor minimus and adductor magnus. Tendon at origin larger in *Sciurus*, *Tamiasciurus*, and *Glaucomyss*. Arises on level with dorsal part of ventral ischial tuberosity in *Glaucomyss* and inserts near middle of femur.

Obturator externus.—Arises on lateral margins of obturator foramen and from obturator membrane; fibers converge to point caudal to head of femur; inserts by tendon in deep trochanteric fossa.

ISCHIOTROCHANTERIC GROUP. Obturator internus is supplied by a branch of the obturator nerve. The gemelli muscles and quadratus femoris are innervated by branches of the tibial nerve.

Obturator internus.—Arises on medial surfaces of ischium caudal and dorsal to obturator foramen; fibers converge to a long tendon, which passes through lesser sciatic notch behind ischial spine; inserts on trochanteric crest and in trochanteric fossa.

Gemellus superior.—Synonym: jumeaux antérieur, Alezais, 1900. Arises on ischial spine and on dorsal surface of ischium from spine to level of acetabulum; situated

caudal to gluteus medius, deep to piriformis, and cranial to gemellus inferior; fibers run laterad to insert on tendon of obturator internus and in trochanteric fossa cranial to tendon.

Gemellus inferior.—Synonym: jumeaux postérieur, Alezais, 1900. Arises from lesser sciatic notch; runs craniolaterad; inserts on tendon of obturator internus and on proximal part of trochanteric fossa and crest. Situated dorsal to quadratus femoris and caudal to gemellus superior.

Quadratus femoris.—Synonym: carré crural, Alezais, 1900. Arises on craniovenral part of quadrilateral area of ischium between dorsal tuberosity and origin of obturator externus; runs deep to origins of caudofemoralis, semimembranosus, and gemellus inferior; inserts on intertrochanteric line on caudal surface of femur from proximo-caudal tip of lesser trochanter to depression between gluteal tuberosity and greater trochanter.

HAMSTRING GROUP. Innervated by branch of tibial nerve.

Caudofemoralis.—Synonyms: adductor magnus (part)?, Hoffmann and Weyenbergh, 1870; adductor 4, Parsons, 1894; ischio-condylien, Alezais, 1900; semimembranosus anticus, Peterka, 1937. Arises along lateral and ventral borders of dorsal ischial tuberosity and on dorsal one-third of ramus of ischium internal to origins of semimembranosus and gemellus inferior and caudal to origin of quadratus femoris. Runs distad cranial to semimembranosus, caudal to adductors, and medial to femorococcygeus. Divides into two parts: lateral part smaller than medial part, inserts by fascia on caudal surface of distal end of femur in depression proximal to lateral epicondyle and on lateral ridge; medial part inserts on caudal border of medial epicondyle and in depression proximal thereto.

Semimembranosus.—Synonym: semimembranosus posticus, Peterka, 1937. Arises by broad tendon on caudal border of ischium from dorsal ischial to ventral ischial tuberosity; runs distad ilateral to gracilis, cranial to semitendinosus, and caudal to caudofemoralis; inserts by fascia on medial side of knee and proximal end of tibia internal to insertion of sartorius and cranial to insertion of gracilis, and on caudal margin of medial tuberosity of tibia by a tendon that runs deep to tibial collateral ligament.

Semitendinosus.—Arises by two heads. Vertebral head smaller; arises in fascia over first two caudal vertebrae; covers ischial head and unites with it by tendinous inscription near middle. Ischial head arises from caudolateral part of dorsal ischial tuberosity in contact with origin of biceps femoris; runs on caudal border of thigh and medial to leg; inserts by broad and short tendon on cranial crest slightly distal to middle of tibia. Inserts nearer knee in *Sciurus*, *Tamiasciurus*, *Neotamias* and *Glaucomys*. A third head is present in *Glaucomys*, which arises on side of seventh caudal vertebra and passes cranial under skin to join body of semitendinosus near junction of other two heads. This is a specialization for increasing surface between hind leg and tail.

Biceps femoris.—Arises from craniolateral part of dorsal ischial tuberosity adjacent to origin of ischial head of semitendinosus; covers caudal half of lateral surface of thigh; inserts on cranial border of proximal three-fourths of leg and on lateral tuberosity of tibia. Insertion occupies proximal two-thirds of leg in *Neotamias* and *Tamiasciurus*, one-half in *Sciurus*, and less than one-half in *Glaucomys*.

FLEXOR GROUP OF LEG. Supplied by tibial nerve.

Gastrocnemius.—Arises by two heads. Lateral head arises by tendon on sesamoid bone located in depression proximal to lateral condyle of femur; sesamoid attached to femur by ligament; arises on sesamoid caudolateral to origin of plantaris and caudomedial to origin of soleus. Medial head over twice as large as lateral head; arises on sesamoid located in depression proximal to medial condyle of femur. Heads unite proximal to middle of leg; body covers caudomedial surface of leg; fibers twist laterad and distad and converge to a broad, flat tendon about one-fourth length of leg from

distal end. Tendon joins tendon of soleus to form tendo calcaneus, which inserts in groove in tuberosity of calcaneus. In *Neotamias*, *Sciurus*, *Tamiasciurus*, and *Glaucomys* the tendons at origin of lateral head and tendo calcaneus are relatively longer and lateral head is more closely attached by fibers to soleus and plantaris near origin.

Plantaris.—Synonyms: flexor digitorum pedis brevis (part), Hoffmann and Weyenbergh, 1870; plantaire grêle, Alezais, 1900. Arises on lateral sesamoid of knee; runs distad deep to gastrocnemius and medial to soleus; ends in strong tendon shortly proximal to calcaneus. Tendon passes superficial to tendo calcaneus on caudomedial surface of calcaneus, where it becomes broader and heavier, and extends to plantar surface in close association with metatarsal pad; at proximal end of metatarsus tendon divides into four tendons, which diverge to bases of second through fifth digits. Tendons to second, third, and fourth digits are perforated; insert on processes on sides of proximal ends of second phalanges. Tendon to fifth digit inserts on proxomedial end of second phalanx. Plantaris is more closely connected with soleus and gastrocnemius at origin in *Neotamias*, *Sciurus*, *Tamiasciurus*, and *Glaucomys*.

Soleus.—Smallest of superficial flexors. Arises by two heads. Femoral head arises on lateral sesamoid of knee; fibular head arises by tendon from proximocaudal surface of head of fibula caudal to attachment of fibular collateral ligament and origin of peroneus longus. The two heads remain separate for two-thirds length of leg; femoral head inserts principally on sheath of fibular head but some fibers reach tendo calcaneus. Tendon of fibular head unites with that of gastrocnemius to form tendo calcaneus, which inserts on tuberosity of calcaneus. Tendon at origin of fibular head longer and femoral head more closely attached to plantaris and gastrocnemius in tree and flying squirrels and chipmunks.

Popliteus.—Arises by tendon from popliteal fossa on lateral epicondyle of femur; tendon passes internal to fibular collateral ligament and caudal to head of tibia; inserts on popliteal surface of tibia. A small sesamoid is present at junction of body and tendon at origin.

Flexor digitorum tibialis.—Synonyms: flexor longus digitorum, Parsons, 1894; fléchisseur tibial, Alezais, 1900; flexor digitorum longus, Peterka, 1937. Arises by fibers on medial ridge from popliteal surface to point one-sixth distance from distal end of tibia and from popliteus and fascia of tibialis posterior. Ends in tendon which passes in groove on medial edge of medial malleolus of tibia in common with tendon of tibialis posterior; tendon runs distad on medial margin of tarsus to medial sesamoid, which lies in tendon, and continues along medial surface of abductor hallucis. Inserts on medial side of proximal end of first phalanx of hallux. A branch tendon inserts in distomedial part of metatarsal pad in *Marmota*. Tendon has slight attachment to medial sesamoid in *Glaucomys*.

Tibialis posterior.—Arises by two short heads; one arises in caudal fossa, and other arises from medial margin of head of fibula; both heads are deep to popliteus. Body attaches on proximal half of lateral border of medial ridge; ends in tendon about two-fifths of distance from distal end of tibia. Tendon runs distad in groove on medial side of medial malleolus with that of flexor digitorum tibialis; inserts on proximal part of tarsale mediale.

Flexor digitorum fibularis.—Synonyms: flexor digitorum pedis communis longus, Hoffmann and Weyenbergh, 1870; flexor longus hallucis, Parsons, 1894; fléchisseur peronier, Alezais, 1900. Arises by two heads; one in proximal part of caudal fossa of tibia; other on medial and caudal surfaces of proximal end of fibula except for origin of tibialis posterior. Body arises in caudal fossa, on interosseous ridge and membrane, on entire caudal surface of tibia, and on medial and caudal surfaces of fibula; ends in strong tendon medial to tuberosity of calcaneus. Tendon passes in deep groove on caudal surface of medial malleolus and divides into five parts below metatarsus; these five tendons run to bases of the digits, through perforations in tendons of plantaris, and along plantar surfaces of digits to insert on ungual phalanges.

Quadratus plantae.—Synonyms: flexor digitorum pedis brevis (part), Hoffmann and Weyenbergh, 1870; accessorius, Parsons, 1894, Alezais, 1900. Arises by fibers on caudal surface of trochlear process and on body of calcaneus distal to origins of abductor digiti quinti and abductor ossis metacarpi quinti, which run external to its proximal end. Fibers run distomedial and merge into a tendon as broad and as long as body of muscle. Inserts on cranial surface of tendon of flexor digitorum fibularis shortly before it divides into five tendons. Fibers extend nearly to insertion in *Neotamias*, *Sciurus*, and *Glaucmys*, and a special tendon runs from distolateral margin of muscle to insert on side of tendon of plantaris to fifth digit; in *Tamiasciurus* the special tendon goes to tendon of plantaris to fourth digit.

FLEXOR GROUP OF PES. Supplied by lateral and medial plantar branches of the tibial nerve.

Flexores digitorum breves.—Two; arise at junction of tendon of quadratus plantae with tendon of flexor digitorum fibularis and on plantar surface of the latter. Situated below lumbricales. Tendons fuse with those of plantaris to third and fourth digits. In *Sciurus* and *Tamiasciurus* fibers attach directly to tendons of plantaris. In *Glaucmys* there are three muscles; medial two are as in *Otospermophilus*; lateral one attaches directly to tendon of quadratus plantae, which joins the tendon of plantaris to fifth digit.

Abductor hallucis.—Arises by short tendon from plantar surface of navicular and by fibers from tip of medial sesamoid; runs distad lateral to tendon of flexor digitorum tibialis, to which it is closely attached; inserts by tendon on medial sesamoid at first metacarpo-phalangeal joint.

Abductor ossis metacarpi quinti.—Arises on caudolateral side of plantar surface of body of calcaneus lateral to origin of abductor digiti quinti; mostly ligamentous; inserts on lateral tuberosity at proximal end of fifth metatarsal medial to insertion of peroneus brevis. In *Marmota* insertion is by two tendons; one normal and other inserts on lateral sesamoid at base of first phalanx of fifth digit. Entirely ligamentous in *Ammospermophilus* and *Cynomys*. More fibers present in *Sciurus*, *Tamiasciurus*, *Neotamias*, and *Glaucmys*.

Abductor digiti quinti.—Synonym: abductor minimi digiti, Parsons, 1894. Arises by fibers on medial and plantar surface of body of calcaneus and on tendon of abductor ossis metacarpi quinti. Runs below trochlear process of calcaneus. Fibers extend to proximal end of fifth metatarsal from whence a tendon runs distad on lateral side of fifth metatarsal. Inserts on proximalateral part of base of first phalanx of fifth digit. Inserts on lateral sesamoid in *Sciurus*.

Lumbricales.—Four; arise from tendon of flexor digitorum fibularis before it divides into tendons and on sides of tendons after division; insert by small tendons on medial sides of proximal ends of first phalanges of second through fifth digits and along digits to joints between first and second phalanges. Five lumbricales present in one specimen of *Marmota flaviventer*.

Adductor hallucis.—Arises by fascia on plantar surface of first metacarpal; runs distad laterad to first metacarpal and flexor hallucis brevis; inserts by tendon on cranio-lateral and proximal surfaces of first phalanx of hallux.

Adductor digiti quinti.—Synonym: adductor minimi digiti, Parsons, 1894. Arises by fascia on plantar surface below third cuneiform; runs below interossei obliquely distolaterad to fourth digit; inserts by tendon on medial side of proximal end of first phalanx of fifth digit.

Flexor hallucis brevis.—Arises on distal tip of plantar surface of first cuneiform and on adjacent fascia; runs on plantar surface of first metatarsal deep to abductor hallucis; inserts on cranial surface of lateral sesamoid at first metacarpo-phalangeal joint. Absent in one specimen of *Marmota flaviventer*.

Interossei.—Eight; two on plantar surface of each of the digits except the hallux. First and second arise by tendon on plantar surface of first cuneiform and by fibers from cartilage caudal to proximomedial tip of first metacarpal; third and fourth arise from third cuneiform; fifth through eighth arise on cuboid on ridge proximal to sulcus for tendon of peroneus longus. All insert on proximal and dorsal margins of sesamoids at second through fifth metacarpo-phalangeal joints.

Paleontology

List of North American Fossil Sciuridae

UPPER EOCENE

Sciurid ? sp. Wilson, 1934:16; Las Posas Sespe of California.

LOWER MIOCENE

Sciurus tecuensis, new species; Tecuya of California.

Sciurus vortmani Cope, 1879:1; John Day of Oregon.

Sciurus ballovianus Cope, 1881:177; John Day of Oregon.

UPPER MIOCENE

Sciurid ? sp. Scharf, 1935:104; Sucker Creek of Oregon.

Protospermophilus angusticeps (Matthew), Matthew and Mook, 1934:4; Deep River of Montana.

Protospermophilus malheurensis (Gazin), 1932:56; Skull Spring of Oregon.

Protospermophilus tephros (Gazin), 1932:59; Skull Spring of Oregon.

Citellus primitivus, new species; Lower Madison Valley of Montana.

Citellus ridgwayi Gazin, 1932:61; Skull Spring of Oregon.

Tamias (Neotamias) ateles (Hall), 1930:314; Barstow of California.

Palaearctomys montanus Douglass, 1903:183; Lower Madison Valley of Montana.

Palaearctomys macrorhinus Douglass, 1903:184; Lower Madison Valley of Montana.

Arctomyoides arctomyoides (Douglass), 1903:181; Lower Madison Valley of Montana.

LOWER PLIOCENE

Sciurus venturus, new species; Quatal Canyon of California.

Protospermophilus quatalensis (Gazin), 1930:64; Quatal Canyon of California.

Palaearctomys vetus (Marsh), 1871:121; Loup Fork of Nebraska (exact age unknown).

MIDDLE PLIOCENE

Sciurus cf. *aberti* Matthew, 1924:84; Upper Snake Creek of Nebraska (exact age unknown).

Citellus (Otospermophilus) gidleyi, (Merriam, Stock, and Moody, 1925:68; Rattlesnake of Oregon.

Citellus (Otospermophilus) argonautus Stirton and Goeriz, MS; Oakdale of California.

Citellus sp. Kellogg, 1910:427; Thousand Creek of Nevada.

Citellus sp. Wilson, 1936:19; Smiths Valley of Nevada.

Citellus sp. Wilson, 1937a:14; Kern River of California.

Citellid sp. Wilson, 1937:33; Bartlett Mountain of Oregon.

Marmota nevadensis (Kellogg), 1910:422; Thousand Creek of Nevada.

Marmota minor (Kellogg), 1910:425; Thousand Creek of Nevada.

Cynomys sp. Matthew, 1899:66; Republican River of Nebraska (exact age unknown).

UPPER PLIOCENE

Citellus (*Otospermophilus*) *bensoni* Gidley, 1922:122; Benson of Arizona.

Citellus sp. Wilson, 1933:122; Hagerman of Idaho.

Citellus sp. Hibbard, 1937:244; Rexroad of Kansas.

Marmota sp. Gazin, 1936:285; Hagerman of Idaho.

Cynomys sp. Hibbard, 1937: 244; Rexroad of Kansas.

PLEISTOCENE

Sciurus panoli Cope, 1869:174; Wythe County, Virginia.

Sciurus calycinus Cope, 1871:86; Port Kennedy Bone Cave, Chester County, Pennsylvania.

Tamiasciurus tenuidens (Hay), 1920:104; Cavetown, Washington County, Maryland.

Tamias laevidens Cope, 1869:174; Wythe County, Virginia.

Tamias nasutus Brown, 1908:193; Conard Fissure, Newton County, Arkansas.

Citellus cochisei Gidley, 1922:121; Curtis, San Pedro Valley, Arizona.

Citellus taylori Hay, 1921:616; near San Diego, Duval County, Texas.

Citellus tuitus Hay, 1921:627; Val Verde Mine, Arizona.

Marmota arizonae Hay, 1921:627; Coconino County, Arizona.

Marmota arrodens Hay, 1921:611; Chelan County, Washington.

Cynomys niobrarius Hay, 1921:615; Sheridan County, Nebraska.

Fossils of the following existing species have been found in Pleistocene deposits: *Sciurus carolinensis*, *Sciurus griseus*, *Tamiasciurus douglasii*, *Tamiasciurus hudsonicus*, *Tamias* (*Tamias*) *striatus*, *Tamias* (*Neotamias*) *senex*, *Ammospermophilus nelsoni*, *Citellus* (*Otospermophilus*) *beecheyi*, *Citellus* (*Callospermophilus*) *lateralis*, *Citellus* (*Citellus*) *richardsonii*, *Citellus* (*Ictidomys*) *tridecemlineatus*, *Marmota flaviventris*, *Marmota monax*, *Cynomys leucurus*, *Cynomys ludovicianus*, *Glaucomyus volans*, and *Glaucomyus sabrinus*.

Accounts of Species

SCIURID? sp. Wilson

(Pl. 8, fig. d)

Sciurid? sp. Wilson, 1934:16, pl. 1, fig. 3.

Material referred. A fragment of a right mandibular ramus with a broken P_4 ; No. 1513, California Institute of Technology Collection of Vertebrate Paleontology.

Age: Upper Eocene. *Fauna:* Las Posas Sespe. *Locality:* Las Posas Hills, southern part of Ventura County, California.

Remarks.—The features of the mandible are not discernible. As in *Sciurus*, the anterior margin of P_4 is smooth and the cusps are low and rounded. The protoconid and parametaconid are close together, the ectostylid is minute, and the hypoconid is more expanded laterally than is the protoconid. The indentation in the labial surface is V-shaped as in *Otospermophilus* and is separated from the talonid basin by a low ectolophid. The talonid basin is deeper than it is in *Sciurus* and shallower than in *Otospermophilus*. This tooth is typically

sciurid in shape and dental pattern, but it cannot be positively referred to the family Sciuridae.

Measurements of P_4 : greatest length, 1.7; width of trigonid, 1.6; width of talonid, 1.9.

SCIURID? sp. Scharf

Sciurid sp. Scharf, 1935:104.

Material referred. A part of a right mandibular ramus with broken teeth; No. 1779, California Institute of Technology Collection of Vertebrate Paleontology.

Age: Upper Miocene. *Fauna*: Sucker Creek. *Locality*: Sucker Creek, about nine miles north of Rockville, eastern part of Malheur County, Oregon.

Remarks.—The mandibular ramus of the Sucker Creek specimen is relatively heavier than that of North American sciurids and is particularly massive at the level of the anterior end of the masseteric fossa. The fossa terminates anteriorly below M_1 , its ventral crest is barely perceptible, and the fossa is flattened. In Miocene sciurids the dorsal and ventral masseteric crests are prominent and the masseteric fossa is correspondingly deeply concave. The width of the incisor is almost as great as its depth. The cheek teeth are relatively larger than are those of Miocene sciurids. It is clear that the Sucker Creek specimen is not a member of the Family Sciuridae. I have not compared it with other Miocene rodents.

Measurements: depth of ramus below M_1 , 9.7; width of ramus below M_1 , 6.6; depth and width of incisor below diastema, 3.2 and 3.3; alveolar length of mandibular tooth row, 14.9.

Sciurus tecuyensis, new species

(Pl. 8, fig. c)

Sciurid sp. Stock, 1920: 272, fig. 6.

Type. A part of a right mandibular ramus extending from the level of the anterior margin of P_4 to the basal part of the vertical ramus; M_1 and M_2 well preserved; No. 23611, University of California Museum of Paleontology.

Age: Lower Miocene. *Fauna*: Tecuya. *Locality*: East side of Tecuya Canyon, about 35 miles south of Bakersfield, Kern County, California.

Diagnosis. Mandibular ramus massive; crests of masseteric fossa prominent and masseteric fossa deep; masseteric fossa acutely pointed anteriorly and ends below protoconid of M_1 . Teeth brachydont; large protoconulids present on M_1 and M_2 .

Remarks.—Stock (1920:272) described the Tecuya specimen but did not express an opinion about its generic position. The mandibular ramus is relatively stouter than that in Recent sciurids, except the highly specialized marmots and prairie dogs, and is not relatively as deep as in Recent *Sciurus*. The masseteric crests are prominent, and the masseteric fossa ends anteriorly below the protoconid of M_1 . In contrast to the rounded condition in Recent *Sciurus* and the broadly rounded shape in *Otospermophilus*, the anterior tip of the masseteric fossa is acutely pointed and is separated from the main part of the fossa by a low ridge. This suggests that a slip of the masseter lateralis was inserted in front of the main part of the muscle and may represent a step in the forward shift of the masseter muscle from its posterior position in the

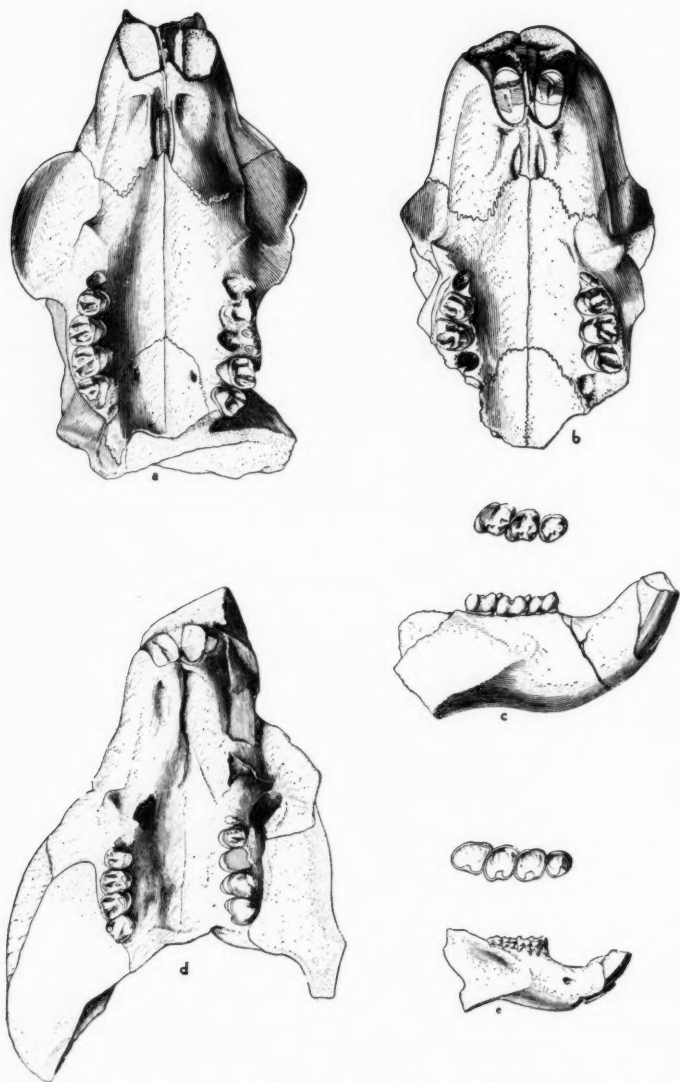


PLATE 7.—a. *Protospermophilus malheurensis* ($\times 2$); no. 129, Calif. Inst. Technology, Collection of Vertebrate Paleontology. b, c. *Protospermophilus quatalensis* ($\times 2$); no. 30, Calif. Inst. Technology, Collection of Vertebrate Paleontology. d. *Citellus ridgwayi* ($\times 2$); no. 334, Calif. Inst. Technology, Collection of Vertebrate Paleontology. e. *Citellus primitivus*. Occlusal view of teeth, $\times 2$; lateral view of mandible, $\times 1$. No. 746, Carnegie Museum, Section of Vertebrate Paleontology.

Paramyidae in which it ends anteriorly below M_2 , to its position below P_4 in Recent sciurids. In the shape of the masseteric fossa and the height of the masseteric crests, the Tecuya specimen is more nearly like *Sciurus* than like any other genus of Nearctic squirrels.

The brachydont cheek teeth are progressively larger from P_4 through M_3 . M_3 is much longer and narrower than M_2 . Other than the size, as determined from the broken roots, nothing can be told about P_4 and M_3 . M_1 and M_2 are rhomboidal in occlusal outline and their dental patterns are similar. The parametaconid is more prominent than the other primary cusps, which are approximately equal in height. A large protoconulid is present on the cranial margin of each tooth and is separated from the protoconid and the parametaconid by shallow furrows. It is closer to the protoconid than to the parametaconid. The hypoconid is expanded at its base and extends farther laterad than does the protoconid. The metalophid on M_2 is represented by a short ridge extending mediad from the protoconid; the shortness may be due to wear, but it is probable that the metalophid was not complete in the unworn condition. The entoconid is a discrete cusp as in Recent *Sciurus*. In terrestrial sciurids and chipmunks the entoconid is not separated from the posterolophid as a discrete cusp. The posterolophid is an uninterrupted, crescentic ridge with no indication of an hypoconulid. Mesoconids and mesostylids are present.

The Tecuya specimen resembles tree squirrels and differs from other living sciurids in the presence of brachydont cheek teeth, the nearly marginal position of the low ectolophid, and the presence of distinct entoconids on M_1 and M_2 . The crescentic posterolophid appears to be a primitive feature which has been retained in terrestrial sciurids and has been modified in Recent tree squirrels. The presence of large protoconulids on M_1 and M_2 is distinctive. Small protoconulids sometimes occur in modern squirrels. Although this specimen has characters which might exclude it from the genus *Sciurus* in a restricted sense, it appears advisable to place it in this genus pending more information about Miocene squirrels and is here named *Sciurus tecuyensis*.

Measurements: depth of ramus below hypoconid of M_1 , 9.8; length of M_1 and M_2 through protoconulid and hypoconid, 3.2, 3.4; length of M_1 and M_2 through parametaconid and entoconid, 2.7, 2.9; width of M_1 and M_2 across trigonid, 2.8, 3.0; width of M_1 and M_2 across talonid, 3.1, 3.2.

SCIURUS VORTMANI Cope

Sciurus vortmani Cope, 1879:1; Cope, 1880:370; Cope, 1881a:363; Cope, 1881b:586; Cope, 1883:50, fig. 4g,h; Cope, 1885:816, pl. 63, fig. 4; Gazin, 1932:58; Wood, 1937:172.

Sciurus vortmani Matthew, 1899:62.

Prosciurus vortmani Matthew, 1909:107; Matthew, 1910:63.

Type. A left mandibular ramus bearing P_4 and M_3 , the anterior tip and the vertical ramus posterior to the bases of the processes absent; No. 6960; American Museum of Natural History. Not seen by the author.

Age: Lower Miocene. *Fauna*: John Day. *Locality*: John Day Valley, Oregon.

Diagnosis.—Mandibular ramus about the size of that of *Sciurus tecuyensis*, deep in

comparison with length; dorsal and ventral masseteric crests prominent; masseteric fossa deep, rounded anteriorly, terminates below the posterior part of M_1 .

Remarks.—The mandibular ramus is deep in comparison with its length, and the base of the coronoid process arises opposite the posterior part of M_3 . The cheek teeth progressively increase in size from P_4 through M_3 . They are subquadrate in occlusal outline, are low crowned, and have shallow talonid basins. The incisors are compressed.

The mandibular ramus of *Sciurus vortmani* is larger and stouter than that of *S. ballovianus*, and the masseteric fossa does not extend as far forward; it approaches *S. tecuyensis* in size, but the masseteric fossa is rounded anteriorly rather than pointed and ends farther posteriad. Also, there is no accessory rugosity for the attachment of a slip of the masseter muscle anterior to the masseteric fossa proper.

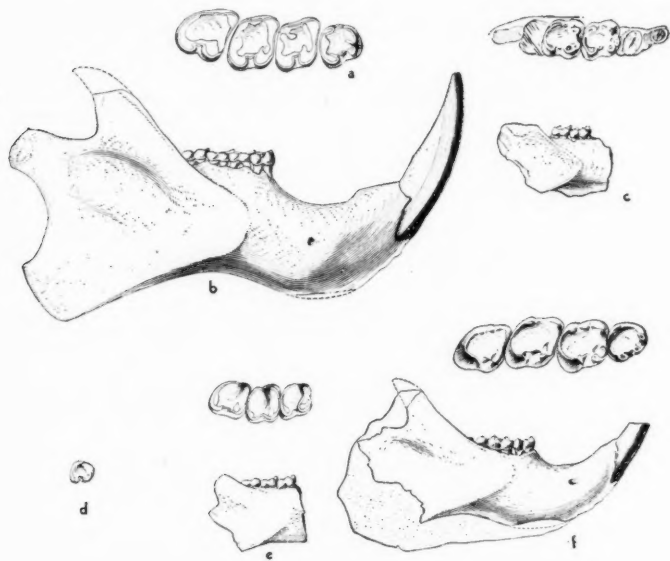


PLATE 8.—a. *Palaearctomys macrorhinus* ($\times 2$); no. 740, Carnegie Museum, Section of Vertebrate Paleontology. b. *Palaearctomys macrorhinus*, composite of left and right mandibular rami ($\times 1$); no. 740, Carnegie Museum, Section of Vertebrate Paleontology. c. *Sciurus tecuyensis*. Occlusal view of teeth, $\times 2$; lateral view of mandible, $\times 1$; no. 23611, Univ. Calif., Museum of Paleontology. d. *Sciurid* sp. ($\times 2$); no. 1513, Calif. Inst. Technology, Collection of Vertebrate Paleontology. e. *Sciurus venturus*. Occlusal view of teeth, $\times 2$; lateral view of mandible in reverse, $\times 1$. No. 34550, Univ. Calif., Museum of Paleontology. f. *Arctomyoides arctomyoides*. Occlusal view of teeth, $\times 2$; lateral view of mandible in reverse, $\times 1$. No. 741, Carnegie Museum, Section of Vertebrate Paleontology.

Matthew (1910:63) placed this species in the genus *Prosciurus* because the masseteric fossa had not assumed the "true sciurid" condition. Wood (1937:172-173) states: "These forms [*S. vortmani* and *S. ballovanus*] have the typical sciurid tooth pattern and the typical zygomasseteric construction."

Measurements (after Cope, 1885:817): depth of ramus at diastema, 5.5; depth of ramus at M_2 , 9.5; alveolar length of mandibular tooth row, 10.0; length of P_4 , 2.4; length of M_3 , 3.0.

SCIURUS BALLOVIANUS Cope

Sciurus ballovanus Cope, 1881:177; Cope, 1881a:363; Cope, 1881b:586; Cope, 1883:50, fig. 4a-d; Cope, 1885:818, pl. 63, figs. 5, 5a, 6, 6a; Trouessart, 1897:425; Matthew, 1899:62; Trouessart, 1904:318; Matthew, 1910:63; Gazin, 1932:58; Wood, 1937:172.

Prosciurus ballovanus Matthew, 1909:107.

Type. A skull, with M^1 and M^2 and without the occipital region, and parts of right and left mandibular rami; No. 6961; American Museum of Natural History. Not seen by the author.

Age: Lower Miocene. *Fauna:* John Day. *Locality:* John Day Valley, Oregon.

Diagnosis. Small size. Skull flattened dorsally and wide interorbitally; muzzle short and narrow; infraorbital foramen a narrow slit; masseteric fossa ends anteriorly below anterior margin of M_1 ; mental foramen near dorsal border of posterior part of diastema. Anterior cingula of M^1 and M^2 large, posterior cingula small; incisors strongly compressed.

Remarks.—*S. ballovanus* is smaller than the other sciurids known from the Lower Miocene. The flattened cranium is characteristic of the Miocene species of squirrels. The cranium is more inflated in the Pliocene and Recent species. The broad interorbital region has been retained by *Sciurus* until the present time.

Measurements (after Cope, 1885:819): length of skull to orbit, 9.0; width between orbits, 9.0; width of muzzle, 4.7; width between last molars, 4.0; length of mandibular ramus, 15.0; length of mandibular diastema, 3.0; elevation of mandibular ramus at coronoid process, 8.0; depth of mandibular ramus at M_1 , 4.5; length of maxillary tooth row, 5.4; length and width of M^1 , 1.5, 1.6; width of upper incisor, 1.3; length of mandibular tooth row, 7.0.

Sciurus venturus, new species

(Pl. 8, fig. c)

Type. A part of a left mandibular ramus extending from the level of the anterior margin of M_1 to the base of the vertical ramus, lower molar teeth well preserved; No. 34550, University of California Museum Paleontology.

Age: Lower Pliocene. *Fauna:* Cuyama. *Locality:* Ravine off north side of Apache Canyon, eight miles northeast of Cuyama Valley in Sec. 2, T. 8 N., R. 23 W., San Bernardino Base and Mer., Ventura County, California.

Diagnosis. Mandibular ramus about the size of that of *S. carolinensis*. Ramus wide in comparison with depth, stout as in *S. tecuensis*; dorsal and ventral masseteric crests prominent; masseteric fossa deep, acutely pointed anteriorly, terminates below P_4 . Lower incisor relatively wider than in Recent *Sciurus*, oval in cross section; lower molars relatively broader than those of comparable Miocene species and relatively narrower than those of Recent *Sciurus*; posterolophids slightly concave anteriorly.

Remarks.—The mandibular ramus of *S. venturus* is relatively stouter than that of *S. tecuyensis* and its depth is less. It resembles *S. tecuyensis* in the strong development of the masseteric crest and the acutely pointed anterior end of the masseteric fossa, but it lacks the subsidiary anterior fossa which is present in *S. tecuyensis*. The fossa ends anteriorly below P_4 as in Recent *Sciurus*.

The lower incisor is broadly oval in cross section and is less compressed than in Recent *Sciurus*. The lower molars are brachydont, the cusps are low and rounded, the ectolophids are situated near the labial margins of the teeth, and the talonid basins are broad and shallow. Small mesoconids and minute mestostylids are present. The ectoconids are discrete cusps, and the entoconid region of M_3 is well developed as in Recent *Sciurus*. In the existing genera of terrestrial sciurids the entoconids are not distinct cusps and the entoconid region of M_3 is reduced in size. The posterolophids of M_1 and M_2 in *S. venturus* are slightly crescentic and thus show a condition transitional between that of the primitive and existing species of *Sciurus*. In the latter the posterolophids are straight. M_1 and M_2 are smaller than in *S. tecuyensis* and are relatively broader than in the Miocene species of *Sciurus*.

The mandibular ramus of *Sciurus venturus* has retained the primitive stoutness and the prominence of the masseteric crests, but it has the modern teeth and anterior position of the masseteric fossa characteristic of Recent forms.

Measurements: depth of ramus below hypoconid of M_1 , 8.1; width of ramus below M_1 , 4.3; greatest length of M_1 , M_2 , and M_3 , 2.6, 2.8, and 3.5; width of M_1 , M_2 , and M_3 across trigonid, 2.5, 3.2, and 3.1; width of M_1 and M_2 across talonid, 2.8 and 3.2.

SCIURUS cf. ABERTI Woodhouse

Sciurus cf. aberti Matthew, 1923:12; Matthew, 1924:84; Wilson, 1937:36.

Material referred. A lower jaw; No. 17578, American Museum of Natural History. Not seen by the author.

Age: Middle Pliocene. *Fauna:* Upper Snake Creek. *Locality:* About 20 miles south of Agate, Sioux County, Nebraska.

Remarks.—In regard to this specimen, Matthew (1924:84) states: "A well-preserved lower jaw, A. M. N. H. No. 17578, from Quarry No. 1, Upper Snake Creek beds is not distinguishable from the jaw of the modern *S. aberti*, but is almost equally like any other of the large western black squirrels. It is a little too large, too deep-jawed and heavy-toothed for the common eastern gray squirrel."

PROTOSPERMOPHILUS Gazin

Type.—*Protospermophilus quatalensis*; No. 30, California Institute of Technology Collection of Vertebrate Paleontology.

Diagnosis.—Dorsal crests of zygomatic plates terminate anteriorly on sides of rostrum well below dorsal surface; ridges on sides of premaxillae lateral to incisors prominent and continuous with dorsal crests of zygomatic plates; mas-

seteric tubercle small; notches in ventral border of zygomatic plates opposite P_4 or line of contact between P_4 and M_1 .

PROTOSPERMOPHILUS MALHEURENSIS (Gazin)

(Pl. 7, fig. a)

Sciurus malheurensis Gazin, 1932:56, pl. 1, figs. 1 and 1a, pl. 2, fig. 3; Scharf, 1935:102.

Type. A skull without the nasal bones, zygomatic arches and the region posterior to the postorbital processes; the incisors, third premolars, and left P_4 and M^1 missing; the other cheek teeth well preserved. No. 129, California Institute of Technology Collection of Vertebrate Paleontology.

Material referred. A poorly preserved skull without teeth, zygomatic arches, and anterior end of rostrum; No. 333, California Institute of Technology Collection of Vertebrate Paleontology.

Age: Upper Miocene. *Fauna:* Skull Spring. *Locality:* Twenty-eight miles south of Harper and approximately three miles northwest of Skull Spring, Malheur County, Oregon.

Diagnosis. Skull about the size of that of *Protospermophilus angusticeps*. Cranium small and flattened dorsally; rostrum massive, depth much greater than width; palate broad; interorbital region broad; dorsal crest of zygomatic plate terminates anteriorly below a rounded bulge at premaxillary-maxillary suture; fossae anterolateral to incisive foramina deep. Cheek teeth small in comparison with size of skull; anterior cingulum on P_4 small; shallow grooves present on lingual margin of each molar at junction of cingula with protocone.

Remarks.—Three Upper Miocene sciurids, here referred to *Protospermophilus*, have been called *Sciurus*. These are *S. malheurensis*, *S. angusticeps*, and *S. tephros*. Several of the features of these animals clearly show that the affinities are with the ground squirrels rather than with the tree squirrels. The zygomatic plate is narrow and concave and terminates dorsally in a marked depression at or posterior to the level of the premaxillary-maxillary suture. The dorsal crest of the zygomatic plate is prominent and particularly so where the dorsal head of the maxillonasalis muscle arises in existing ground squirrels; this head of the maxillonasalis and the crest at its origin are absent in tree squirrels. The infraorbital foramen is situated near P^3 and is nearly vertical. The masseteric tubercle is immediately beneath the foramen. The premaxillary-maxillary suture runs past the cranial tip of the dorsal crest of the zygomatic plate and turns ventrad well in front of the level of the infraorbital foramen. Depressions anterolateral to the incisive foramina are present. These depressions are indicative of the presence of cheek pouches (see page 268) and when large provide positive evidence of the presence of these pouches. The lophs of the upper cheek teeth are convergent, and the teeth are triangular or subquadrate in occlusal outline. In view of these similarities to ground squirrels and differences from tree squirrels, it is difficult to see why these animals were originally referred to *Sciurus*. The rostrum and the incisors are deep as in living tree squirrels, but I have been unable to discover other characters in which these fossil squirrels resemble tree squirrels and differ from terrestrial sciurids.

The Miocene squirrels, incorrectly called *S. malheurensis*, *S. angusticeps*, and *S. tephros*, resemble *Citellus quatalensis*, for which the subgenus *Protospermophilus* was established by Gazin (1930:64), and differ from living and other fossil terrestrial sciurids in several respects. The dorsal crest of the zygomatic plate terminates anteriorly well below the dorsal surface of the rostrum. The incisors are heavier than in existing ground squirrels and, as a result, the rounded ridges on the premaxillae lateral to the incisors are more prominent. Furthermore, these ridges are continuous with the dorsal crest of the zygomatic plates rather than situated below the dorsal crests as in existing ground squirrels. Actually, the incisors are in the same relative positions, but the plates are lower and consequently smaller in the fossil forms. The masseteric tubercles are small. The notches in the ventral borders of the zygomatic plates are opposite P^4 or the P^4 - M^1 contact line. All of these differences between the fossil and Recent ground squirrels are correlated with the increase in the size of the masseter superficialis and the masseter lateralis pars anterior in the Recent forms. *Protospermophilus quatalensis*, from the Lower Pliocene, has larger masseteric tubercles than the Miocene forms. The characteristics distinguishing these four fossil forms from other sciurids are considered to be of generic value. *Protospermophilus* is accordingly raised from subgeneric to generic rank and is characterized by the above mentioned features. The characterization above differs from that originally given by Gazin (1930:64). The forms previously named *Sciurus malheurensis*, *Sciurus angusticeps*, *Sciurus tephros*, and *Citellus quatalensis* are here assigned to the genus *Protospermophilus*.

A comparison of *P. malheurensis* with *P. angusticeps* reveals the following differences: cranium less inflated, rostrum narrower and deeper in relation to its length, masseteric tubercle larger, tympanic bullae relatively smaller, occipital region of skull narrower, and cheek teeth smaller. As in Recent terrestrial forms the lateral pterygoid plate extends posteriad nearly to the tympanic bulla and the pterygoid fossa is large.

In *P. malheurensis*, P^3 is a simple cone about two-fifths as large as P^4 . The other cheek teeth are low crowned, but the valleys are deeper than they are in the cheek teeth of Recent *Sciurus*. The anterior and posterior cingula are nearly parallel. They bend sharply to join the protocone, and shallow furrows are present at their junctions with the protocone. Similar furrows are present on the cheek teeth of *P. quatalensis* and may be characteristic for the genus. On P^4 , M^1 , and M^2 the proto-lophs and metalophs converge toward the protocone, and the metalophs are low and constricted between the protocones and metaconules. M^1 and M^2 are subquadrate in occlusal outline, are larger than P^4 , and have large parastyles. M^3 is smaller than M^2 , and is triangular in occlusal outline. A low metaconule is present on M^3 , but the metaloph is barely perceptible. Mesostyles are present on P^4 through M^3 .

Measurements: No. 333: distance from posterior margin of incisive foramen to tip of occipital condyle, 44.2; depth of muzzle below nasofrontal suture, about 15.3; greatest width of cranium not including zygomatic portion of squamosal, about 21.3; width across anterior ends of tympanic bullae, 19.8; anteroposterior length of bullae, 11.0; depth from middorsal point of superior nuchal line to level of ventral surfaces

of tympanic bullae, 17.5; shelf of bony palate, about 20.6. No. 129: depth of muzzle below nasofrontal suture, 16.1; width of dorsal surface of muzzle above anterior ends of incisive foramina, 7.7; length of upper diastema, 15.4; distance between posterior margin of incisive foramen and P3, 9.9; width of palate between first molars, 8.2; depth of skull above posterior end of bony palate, 15.9; alveolar length of maxillary tooth row, 10.5; length of alveolus of P3, 1.4; depth and width of upper incisor, 4.3 and 2.4; greatest length of P4, M1, M2 and M3, 2.0, 2.4, 2.4, and 2.5; greatest width of P4, M1, M2, and M3, 2.4, 2.7, 2.8, and 2.5.

PROTOSPERMOPHILUS ANGUSTICEPS (Matthew)

Sciurus angusticeps Matthew, Matthew and Mook, 1933:4, fig. 2.

Type. A skull without the left zygomatic arch, third premolars, left M2, and third molars; No. 21336, American Museum of Natural History. Not seen by the author.

Age: Upper Miocene. *Fauna:* Deep River. *Locality:* Seven miles southeast of Fort Logan, Meagher County, Montana.

Diagnosis. Skull near the size of that of *P. malheurensis*; larger than that of *P. tephros*. Cranium moderately inflated, about as in *Otospermophilus*; rostrum relatively broader than in *P. malheurensis* and relatively narrower than in *P. quatalensis*; palate broad; notch in ventral border of zygomatic plate opposite P4. P3 larger than in *P. quatalensis*; other cheek teeth large. The diagnosis given by Matthew (1933:4) is primarily generic rather than specific.

Remarks.—The relationships of *P. angusticeps* are considered in the discussion of *P. malheurensis* on page 348.

PROTOSPERMOPHILUS TEPHRUS

Sciurus tephros Gasin, 1932:59, pl. 1, figs. 2, 2a, 2b; Scharf, 1935:102.

Type. A skull without the zygomatic arches, the posterior part of the cranium, and the left cheek teeth; incisors broken off at alveoli. No. 332, California Institute of Technology Collection of Vertebrate Paleontology.

Age: Upper Miocene. *Fauna:* Skull Spring. *Locality:* Twenty-eight miles south of Harper and approximately three miles northwest of Skull Spring, Malheur County, Oregon.

Diagnosis. Skull small and slender. Rostrum slender, depth greater than width; ridges on premaxillae lateral to incisors low; interorbital region narrow; fossa on anterior surface of zygomatic plate small; notch in ventral border of zygomatic plate opposite posterior margin of P4; fossae anterolateral to incisive foramina shallow.

* *Remarks.*—The relationships of *P. tephros* are considered in the discussion of *P. malheurensis* on page 348.

P. tephros is a small form approaching *Sciurus ballovianus* in size. The rostrum is relatively long, narrow, and deep. The zygomatic plate is narrow and its ventral border is opposite the posterior margin of P4. The longitudinal swellings on the sides of the rostrum are not as prominent as those in *P. quatalensis*. The fossae anterolateral to the incisive foramina are smaller than are those in *P. malheurensis*. The upper diastema is long in proportion to the size of the skull.

The upper incisors are compressed. The cheek teeth are heavily worn and some of the features of the dental pattern are obscured. P3 appears to be absent. P4 is small and compressed anteroposteriorly; the anterior cingulum

is minute and the posterior cingulum is absent. On M¹ and M² the occlusal outline is subquadrate, the cingula are small, the protoloph and metalophs converge toward the protocones, and mesostyles are present. On M³ the anterior cingulum is small, the protoloph is well developed, and the metaloph is not visible.

Measurements: distance from dorsal margin of alveolus of upper incisor to most anterior point of orbit, 10.9; depth of muzzle below nasofrontal suture, about 11.5; length of diastema between upper incisor and P⁴, 12.4; distance between posterior margin of incisive foramen and P⁴, about 7.0; shelf of bony palate, about 14.5; depth of skull above posterior margin of bony palate, about 13.3; alveolar length of maxillary tooth row, 6.9; depth of and width of upper incisor, 2.9, 1.6; greatest length of P⁴, M¹, M², and M³, 1.4, 1.8, 1.8, and 2.1; greatest width of P⁴, M¹, M², and M³, 1.8, 2.1, 2.2, and 2.0.

PROTOSPERMOPHILUS QUATALENSIS (Gazin)

(Pl. 7, figs. b, c.)

Citellus (Protospermophilus) quatalensis Gazin, 1930:64, pls. 1, 2;
Gazin, 1932:62; Howell, 1938:214.

Type. A skull without the cranium and the posterior half of the orbits, broken upper incisors and left P³ through M² present; a left mandibular ramus with lower incisor, P⁴ and M¹, and without the mandibular processes; the central third of a right mandibular ramus with M¹ and M²; No. 30, California Institute of Technology Collection of Vertebrate Paleontology.

Material referred. Nos. 31 and 32, California Institute of Technology Collection of Vertebrate Paleontology; No. 31, the central part of a left mandibular ramus with P⁴, M¹, and M²; No. 32, a fragment of a left mandibular ramus with all of the cheek teeth.

Age: Lower Pliocene. *Fauna:* Quatal Canyon. *Locality:* Near intersection of latitude 34° 50' N and longitude 119° 20' W, immediately south of the northern boundary of Ventura County, California.

Diagnosis. Skull massive; width of rostrum greater than depth; ridges on premaxillae lateral to incisors prominent; palate wide in proportion to length of tooth row but actually narrower than in *P. malheurensis* and *P. angusticeps*; fossae anterolateral to incisive foramina deep; masseteric tubercles moderately prominent. Lower jaw shallow and stout; dorsal surface between incisor and P⁴ slightly depressed; masseteric crests prominent; masseteric fossa terminates anteriorly below posterior margin of P⁴. Mandibular tooth row long in proportion to depth of jaw; P³ a minute cone; P⁴, M¹ and M² nearly quadrate in occlusal outline, low crowned, cingula separated from protocone by furrows; mesostyles and mesostylids present on molars.

Remarks.—The affinities of *P. quatalensis* are discussed on pages 348 and 349. It appears that this species is an aberrant type of ground squirrel without close relationships with Recent ground squirrels.

The anterior parts of the skull and the cranium are shallow and flattened dorsally. The premaxillae are expanded dorsally to accommodate the large and sharply curved incisors, and form a greater part of the dorsal surface of the rostrum than in other North American sciurids. Prominent ridges extend along the lateral margins of the premaxillae from the dorsal surface of the zygomatic plates to the alveoli of the incisors. In Recent sciurids the anterior ends of the premaxillae do not appear on the dorsal surface of the rostrum and the lateral

ridges are not as prominent. The rostrum is broad and shallow, as it is in many fossorial rodents. The fossae anterolateral to the incisive foramina are large, as in the existing terrestrial sciurids with large cheek pouches.

The mandible is shallow and heavy, and the diasternal portion is short. The masseteric fossa is deep except at the anterior end, where a separate slip of the masseter seems to have been attached. The anterior end attained the position below P_4 which is characteristic of modern sciurids. The anterodorsal margin of the ramus is as high as the alveolar border. The ramus resembles that of *Citellus primitivus*, but it is smaller and the diasternal portion is relatively heavier.

P^3 is a minute, peglike tooth as in *Sciurus*, *Ammospermophilus*, and *Xerospermophilus*. The cheek teeth are more nearly brachydont than are those of *Citellus primitivus*. The upper cheek teeth are quadrate in occlusal outline and have low cusps and shallow basins. They are thus more primitive than the upper cheek teeth of *Citellus ridgwayi*. The teeth are small in proportion to the size of the skull. The protocone of P^4 , M^1 and M^2 (M^3 is absent) is separated from the buccal ends of the anterior and posterior cingula by shallow grooves, instead of merging imperceptibly with the cingula as in most sciurids. The protomere consequently consists of a smaller anterior part and of subequal medial and posterior divisions. A similar conformation occurs in the upper teeth of *P. malheurensis* and of existing chipmunks and flying squirrels. The protoloph is well developed, have faint indications of protoconules, and extends at right angles to the anteroposterior axis of the teeth. The metalophs bear large metaconules. They extend anteromedial from the metacones and are constricted to narrow bands between the metaconules and protocones. Large mesostyles are present, and on one tooth there are two small styles between the paracone and the metacone. The anterior cingulum on P^4 is small and is not enlarged buccally as it is on M^1 and M^2 ; it is large on M^1 and M^2 , has a prominent parastyle, and curves sharply to join the protocone. The posterior cingulum on P^4 , M^1 and M^2 is small and merges imperceptibly with the metacone; its medial end is expanded into a well-defined hypocone, which is absent or minute in Recent sciurids.

The lower cheek teeth increase in size from P_4 through M_3 . P_4 is trapezoidal in occlusal view, because of the appressed condition of the protoconid and parametaconid. M_1 and M_2 are nearly rhomboidal in occlusal outline. M_3 is longer than wide. The ectolophids are situated well in from the labial margins of the teeth and bear mesoconids. The protolophids and metalophids are uninterrupted until well worn and are lower in the middle than at the ends. Small protoconulids are present near the protoconids. The crescentic postero-lophids terminate medially in low but distinct entoconids. Small mestostylids are present on most of the teeth. The talonid basins are deeper and relatively smaller than are those of *Sciurus* and thus resemble the basins of the teeth of ground squirrels.

Measurements: depth of muzzle in front of maxillae, 10.3; width of muzzle, 14.7; length of upper diastema, 11.4; width of palate between first molars, 8.2; length of palate from incisors to postpalatal notch, 24.9; length of maxillary tooth row, about 10.5; depth and width of upper incisor, 3.4 and 1.9; length and width of P^4 , 2.0 and

2.5; length and width of M^1 , 2.2, and 2.6; length and width of M^2 , 2.3 and 2.7; depth of mandibular ramus under M^1 , 7.3; length of lower diastema, 6.6; length of mandibular tooth row, 10.0; depth and width of lower incisor, 3.1 and 1.6; length and width of P_4 , 1.9 and 1.8; length and width of M^1 , 2.0 and 2.3; length and width of M^2 , 2.4 and 2.7; length and width of M^3 , 3.2 and 2.7.

Citellus primitivus, new species

(Pl. 7, Fig. e)

Sciurus. Douglass, 1903:181, fig. 21; Matthew, 1909: 114 (?).

Type. A right mandibular ramus with a broken incisor, worn cheek teeth, and the basal portion of the vertical ramus; No. 746, Carnegie Museum Section of Vertebrate Paleontology.

Age: Upper Miocene. *Fauna*: Lower Madison Valley. *Locality*: Madison Valley, probably Gallatin County, Montana.

Diagnosis. Size of mandibular ramus near that of *Citellus* (*Otospermophilus*) *variegatus*; ramus relatively stouter and the symphysis broader. Masseteric crests prominent; masseteric fossa concave; acutely pointed anterior end of fossa terminates below hypoconid of P_4 . Lower incisor deep in comparison with width; cheek teeth small in relation to size of ramus.

Remarks.—This mandibular ramus is relatively longer and shallower than that of *Sciurus* and is slightly heavier than the ramus of *Otospermophilus*. The diastemal part of the ramus is slender, the mental foramen is located midway between P_4 and the anterior end of the ramus, and the anterodorsal tip of the ramus is level with the alveolar border. These are features in agreement with *Citellus* and of difference from *Sciurus*. The masseteric fossa is deep because the masseteric crests are high, and it ends anteriorly below the hypoconid of P_4 .

The lower incisor is flatter than it is in *Otospermophilus* but it is not as compressed as in Recent *Sciurus*. The cheek teeth are heavily worn and the dental pattern cannot be determined. As in *Otospermophilus* the indentations in the labial margins of the teeth are deep and narrow, which indicates that the ectolophids were located well in from the margins. The entoconids seem to have been small, and the entoconid regions of the molars are evenly rounded as in ground squirrels. In *Sciurus* the entoconids are distinct cusps and the entoconid regions of the molars are angular. The posterolophids are slightly concave anteriorly. The cheek teeth are small for a jaw of this size.

P. malheurensis and *P. tephros* are not known by mandibles and cannot be directly compared with the Lower Madison Valley specimen. However, if the shape of the mandible in correlation with the shape of the skull in existing sciurids may be used as a criterion, these species are not closely related. Likewise, *Citellus ridgwayi* cannot be directly compared with this specimen.

The evidence shows conclusively that the specimen under consideration was more closely related to the ground squirrels, particularly to *Otospermophilus*, than to the tree squirrels, and indicates that it is near the phyletic line of the former. It is probably subgenerically distinct from *Otospermophilus*.

Measurements: Length of diastema, 9.9; depth of diastemal part of ramus at the level of the mental foramen, 6.5; depth and width of lower incisor, 3.7 and 1.6;

alveolar length of mandibular tooth row, 9.; greatest length of P_4 , M_1 , M_2 , and M_3 , 1.9, 2.2, 2.3 and 2.9; greatest width of P_4 , M_1 , M_2 and M_3 , 2.0, 2.7, 3.0, and 2.6.

CITELLUS (OTOSPERMOPHILUS) GIDLEYI (Merriam, Stock and Moody)

Otospermophilus gidleyi Merriam, Stock and Moody, 1925:68, fig. 23; Gazin, 1930:65; Wilson, 1936:19; Wilson, 1937:33; Wilson 1937a:14; A. H. Howell, 1938:215.

Otospermophilus from the Rattlesnake, Matthew and Mook, 1933:6.

Type. A part of a left mandibular ramus without the anterior tip and the vertical ramus, all of the cheek teeth well preserved; No. 26793, University of California Museum of Paleontology.

Age: Middle Pliocene. *Fauna:* Rattlesnake. *Locality:* Five and one-half miles west of Dayville, Grant County, Oregon.

Diagnosis. The mandibular ramus smaller and mandibular tooth row shorter than in Recent species of *Otospermophilus*. Notches between protoconids and parametacoids shallow; ectolophids submarginal; distinct mesostylids on M_1 and M_2 ; ectotylids on all molars; talonid basins shallow.

Remarks.—The mandibular ramus has the proportions of that of *Citellus beecheyi* but is smaller. The ventral masseteric crest is low and the dorsal one is indistinct. The masseteric fossa is shallow and broadly rounded anteriorly; it terminates below the hypoconid of P_4 . The lower cheek teeth are smaller than in Recent *Otospermophilus* and *Citellus argonautus*. The crowns are low, and the trigonid is slightly higher than the talonid. On P_4 the protoconid and parametacoid are adjacent. The ectolophids are more nearly marginal than in Recent *Otospermophilus*, and the mesoconids are not perceptible.

This species is the oldest known ground squirrel in which the mandible has the features characteristic of modern forms. Differences from the primitive species, *Citellus primitivus* and *Protospermophilus quatalensis*, are as follows: mandible relatively slenderer, masseteric crests lower and masseteric fossa flattened, anterior end of masseteric fossa rounded rather than pointed and consequently occupying a greater part of the lateral surface of the ramus.

Measurements: depth of mandibular ramus below the hypoconid of P_4 , 7.0; alveolar length of mandibular tooth row, 8.4; greatest length of P_4 , M_1 , M_2 , and M_3 , 1.9, 1.9, 2.0, and 3.2; width across trigonid of P_4 , M_1 , M_2 , and M_3 , 1.4, 2.1, 2.2, and 2.4; width across talonid of P_4 , M_1 , M_2 , 2.0, 2.1, and 2.4.

CITELLUS (OTOSPERMOPHILUS) ARGONAUTUS (Stirton and Goeriz)

Otospermophilus argonautus Stirton and Goeriz, 1942:462, fig. 7e.

Type. A fragment of a right mandibular ramus with P_4 and M_1 , and pieces of the pelvis; No. 34281, University of California Museum of Paleontology.

Material referred. A left mandibular ramus without teeth, the condyloid and angular processes missing; No. 34280, University of California Museum of Paleontology.

Age: Middle Pliocene. *Fauna:* Oakdale. *Locality:* Charles E. Schell Ranch, five miles west of Knight's Ferry, Stanislaus County, California.

Diagnosis. Mandibular ramus small, about the size of that of *Citellus gidleyi*; P_4 and M_1 relatively large; M_1 long in relation to width, nearly rhomboidal in occlusal view; mesostylids absent; ectolophids situated well in from labial margin of M_1 . Masseteric crests more prominent than in *C. gidleyi*.

Remarks.—The mandibular ramus, particularly the part below the cheek

teeth, is shallower than in *C. gidleyi* and Recent *Otospermophilus* (*beecheyi* and *variegatus*). P_4 and M_1 are relatively larger than in *C. gidleyi* and they lack mesostylids. M_1 is slightly longer than wide, whereas in Recent *Otospermophilus* it is wider than long. The ectolophid is located well in from the labial margin of M_1 , as in Recent *Otospermophilus*, and the talonid basin is correspondingly reduced in size.

Measurements: No. 34281: depth of ramus below hypoconid of P_4 , 6.5; length of P_4 , 2.5; width of trigonid of P_4 and M_1 , 1.7 and 2.5; width of talonid of P_4 , 2.3.

CITELLUS (OTOSPERMOPHILUS) BENSONI Gidley

Citellus bensoni Gidley, 1922:122, pl. 34, figs. 3, 4; Hay, 1927:136; Gazin, 1932:63; Wilson, 1933:122; Wilson, 1937:39; Schultz, 1937:85; A. H. Howell, 1938:215.

Type. A first or second right upper molar and a left M_3 ; No. 10531, United States National Museum.

Material referred. The cheek teeth in a left mandibular ramus; No. 10532, United States National Museum. Not seen by the author.

Age: Upper Pliocene. *Fauna*: Benson. *Locality*: West of the State Road, about two miles south of Benson, San Pedro Valley, Cochise County, Arizona.

Diagnosis. Length of mandibular tooth row about 10.3. Summit of the right upper molar narrow; anterior cingulum, protoloph, and metaloph about equal in length; metaloph with distinct metacone and metaconule, the latter rounded and not connected to the protocone. Posterior part of M_3 like that of *C. cochisei*. M_3 relatively small as compared with M_3 in living species, and with an isolated metaconule.

Remarks.—*C. bensoni* resembles *C. beecheyi* more closely than it resembles other living species. Gidley (1922:122) states: "In *C. beecheyi* the crowns of the upper molars are relatively narrower than in the fossil species, being nearly as long as wide; the lingual wall of the protocone is less sloping, and the exterior or buccal face of this cusp is much more sloping. Other differences noted in the living species are the generally less broken up condition of the posterior transverse lophs [metalophs]; the somewhat shallower transverse valleys, the posterior one of which usually has a small cusplule [mesostyle] at its external entrance; and the relatively broader and less completely inclosed posterior valley of the last upper molar. Beyond the fact that the last lower molar, like the upper, is relatively smaller, and the valleys and cusps are somewhat more sharply defined than in *C. beecheyi*, there is little to distinguish between the lower cheek teeth of that species and *C. bensoni*."

CITELLUS RIDGWAYI Gazin

(Pl. 7, fig. d)

Citellus ridgwayi Gazin, 1932:61, pl. 2, figs. 1, 1a, 2, 2a; A. H. Howell, 1938:215.

Citellus longirostris Scharf, 1935:102.

Type. The facial region of the skull, including most of the right zygomatic arch and all of the teeth except the right P_3 ; the incisors are broken at the alveoli; No. 334, California Institute of Technology Collection of Vertebrate Paleontology.

Material referred. A skull lacking the occipital region, tympanic bullae, right zygomatic arch, incisors, and premolars; not as well preserved as No. 334; No. 335, California Institute of Technology Collection of Vertebrate Paleontology.

Age: Upper Miocene. *Fauna*: Skull Spring. *Locality*: Twenty-eight miles south

of Harper and approximately three miles northwest of Skull Spring, Malheur County, Oregon.

Diagnosis. Size of skull and length of maxillary tooth row near that of *C. lateralis chrysodeirus*. Skull shallower, cranium less inflated, interorbital region wider, and zygomatic arches more closely appressed to skull than in Recent species. P³ minute; P⁴ short anteroposteriorly because of small size of anterior and posterior cingula.

Remarks.—*C. ridgwayi* possesses the typical ground squirrel zygomatic structure (see page 308), construction of zygomatic arch, and dental pattern. The zygomatic arches do not spread as far laterally as they do in Recent ground squirrels, of which they most closely resemble those of *Ammospermophilus*; and the zygomatic plate slants more nearly horizontally. The dorsal margin of the zygomatic plate continues anteriorly as a low ridge along the contour of the upper incisor. The masseteric tubercle is large and the infraorbital foramen appears to be oval in shape. The cranium is less inflated than it is in modern ground squirrels and thus resembles other Miocene sciurids. The skull is broad interorbitally.

The dental pattern of the cheek teeth is similar to that of Recent ground squirrels with relatively unspecialized dentitions. The cheek teeth are low crowned as in *Otospermophilus* and *Callospermophilus*. P³ is a minute, conical tooth and is smaller than in existing ground squirrels, except *Ammospermophilus* and *Xerospermophilus*. P⁴ is relatively short and broad and appears to have no anterior cingulum. On M¹ and M² the trigon is broadly V-shaped, the metaloph continues from the protocone to metacone without interruption, mesostyles are present, and M³ is slightly larger than M². The anterior cingulum on M³ is smaller than that in existing ground squirrels, and the posterior part of the tooth has the usual expanded hypocone and reduced metaloph.

Most of the features of the skull are primitive and do not permit a definite subgeneric assignment of these fossils. However, the dental pattern, height of crown, and occlusal outline of the cheek teeth are similar to those of *Callospermophilus*; it is on this basis that these fossils are questionably referred to this subgenus.

I quote Gazin (1932:62-63) in regard to the relationships of *C. ridgwayi*: "Compared with *C. (Protospermophilus) quatalensis* Gazin, *C. ridgwayi* is less robust, decidedly smaller and has somewhat more modernized teeth. The two species undoubtedly belong to different subgroups, but their position in the phylogenetic tree is not definitely known. *C. (P.) quatalensis*, although more primitive, comes apparently from younger beds than the species *C. ridgwayi* and hence cannot belong with the latter in the same phyletic line. The resemblances of the two forms, one to *Callospermophilus* and the other to *Otospermophilus*, might suggest their positions in the phylogenetic series. The close relationship existing between these living groups obviates, however, the possibility of an independent origin of the types in less closely related Miocene forms." Since *C. primitivus* is more closely related to Recent *Otospermophilus*, the most primitive subgenus of existing ground squirrels, than is *P. quatalensis*, it appears that the latter species is not in the line of descent of *Otospermophilus*, as was assumed by Gazin, but represents a line which must have diverged from the phyletic line of existing ground squirrels before the Upper Miocene.

Measurements. Nos. 334 and 335: depth of skull from frontal bones to palate between first upper molars,, 9.4; width of palate between first upper molars, about 6.9, 6.9; length of upper diastema, about 13.1,,; greatest length of maxillary tooth row not including P₃, 7.9, about 7.9; depth of upper incisor about 2.8, about 2.7; width of upper incisor, 1.9, about 1.9; greatest diameter of P₃, 0.7,,; greatest length and width of P₄, 1.6 and 2.0,,; greatest length and width of M¹, 1.9 and 2.4, about 1.8 and 2.3; greatest length and width of M², 2.0 and 2.4, 2.0 and 2.3; greatest length and width of M₃, 2.3 and 2.1, 2.2 and 2.0.

CITELLUS sp. L. Kellogg

Citellus sp. L. Kellogg, 1910:427, fig. 8; Merriam, 1911:211, 213, 214, 253; Merriam, 1917:429; Wilson, 1937:34; Wilson, 1937a:14.

Material referred. A worn right M₁ in a fragment of the mandibular ramus; No. 12570, University of California Museum of Paleontology.

Age: Middle Pliocene. *Fauna:* Thousand Creek. *Locality:* Thousand Creek, Humboldt County, Nevada.

Remarks.—The parametaconid and a part of the protoconid of this M₁ are broken off, and the tooth is so badly worn that some of its features are indistinguishable. The ectolophid is located well in from the labial margin, there is no indication of a mesaconid, the hypoconid is small in comparison with the protoconid, and the indentation between the protoconid and hypoconid is broadly U-shaped. The latter feature distinguishes this from *C. gidleyi*, *C. argonautus*, and *Citellus* sp. from Smiths Valley. The tooth is certainly that of a ground squirrel and resembles M₁ of *Callospermophilus* more closely than that in other squirrels.

Measurements of M₁: Length through protoconid and hypoconid, 2.1; width across talonid, 2.3.

CITELLUS sp. Wilson

Citellus? sp. Wilson, 1937a:14, pl. 3, figs. 1, 1a; Wilson 1937:34.

Material referred. The part of a right mandibular ramus between the alveolus of the incisor and the base of the vertical ramus, with heavily worn P₄, M₁, and M₂; No. 1965, California Institute of Technology Collection of Vertebrate Paleontology.

Age: Middle Pliocene. *Fauna:* Kern River. *Locality:* Bakersfield Quadrangle, U. S. Geological Survey, NE ¼ Sec. 26, T. 28S, R. 28E, Mt. Diablo Base and Mer., Kern County, California.

Remarks.—There is no doubt that Wilson's reference of the Kern River specimen to the genus *Citellus* is correct. The mandibular ramus is shallower and weaker than that of *Sciurus* and larger and stouter than that of *Tamias*. The dental pattern is not distinguishable, but the shape and height of the teeth are typical of ground squirrels. The ramus is about the same size and proportions as that of *Citellus* sp. from Smiths Valley, but the masseteric crests are stronger and the mandibular tooth is shorter. M₁ is slightly smaller than in *Citellus* sp. from Thousand Creek and, like that form, has a prominent hypoconid and a U-shaped indentation between the protoconid and hypoconid. *C. gidleyi* approaches the Kern River specimen in the length of the mandibular tooth row and the width of the cheek teeth, but its mandibular ramus is larger in all respects.

The material available does not warrant giving this specimen a specific

name but is sufficient to permit one to conclude that it represents a ground squirrel without the highly specialized dentition of the subgenus *Citellus* and that it is more closely related to *Callospermophilus* or *Ammospermophilus*.

Measurements: depth of ramus below hypoconid of P_4 , 5.5; alveolar length of mandibular tooth row, 8.4; greatest length of P_4 , M_1 , and M_2 , 1.8, 1.9, and 2.0; width of trigonid of P_4 and M_2 , 1.5 and 2.1; width of talonid of P_4 and M_2 , 1.8 and 2.4.

CITELLUS sp. Wilson

Citellus? sp. Wilson, 1933:122, pl. 1, fig. 6; Wilson, 1937:38.

Citellid sp. Schultz, 1937:84.

Material referred. A right P_4 ; No. 12963, United States National Museum. Not seen by the author.

Age: Upper Pliocene. *Fauna*: Hagerman. *Locality*: On Snake River across from Hagerman, Twin Falls County, Idaho.

Remarks.—Wilson (1933:122) writes: "This specimen probably represents a species of *Citellus* in the broader sense and as included in such doubtful genera as *Callospermophilus* and *Otospermophilus*. No. 12963 resembles the comparable tooth in the latter genera decidedly more than it does that in typical *Citellus*."

"The Idaho citellid differs from specimens of *Otospermophilus beecheyi* beecheyi, . . ., in slightly more marginal position of the cusps, in presence of a U-shaped rather than a V-shaped notch between paraconid and internal rim of talonid, in greater definitiveness of paraconid and protoconid, and in smaller size. No. 12963 differs somewhat from specimens of Recent *Callospermophilus lateralis certus* in the more U-shaped notch between paraconid and internal rim of talonid, and in the slightly greater separation of paraconid and protoconid. No. 12963 is slightly larger than P_4 in Recent specimens of *Callospermophilus*."

"The Idaho specimens is distinctively smaller than either of the two fossil citellids described by Gidley from the San Pedro Valley beds." The measurements of this P_4 show that the size of the tooth is nearer that of *Callospermophilus* than of *Otospermophilus*, and is but slightly different from the size of P_4 of *Citellus* sp. from the Kern River fauna.

Measurements (after Wilson, 1933:122): anteroposterior length of P_4 , 1.7; transverse width of P_4 , 2.0.

CITELLUS sp. Hibbard

Citellus sp. Hibbard, 1937:244.

Age: Upper Pliocene. *Fauna*: Rexroad. *Locality*: Meade County, Kansas.

Remarks.—Hibbard (*loc. cit.*) makes the following statement concerning the ground squirrel collected in Meade County: "The genus *Citellus* is represented by two molars, No. 3929 representing a form about the size of *Citellus t. tridecemlineatus*. Also there are five molar teeth, No. 3931 representing a form of *Citellus* larger than *Citellus franklini* [*sic*]. Another form of *Citellus*, intermediate in size, is represented by five molar teeth, No. 3930." These specimens have not been examined by the author.

CITELLUS sp. Wilson

Citellus ? sp. Wilson, 1936:19, pl. 1, fig. 5; Wilson, 1937:34.

Material referred. A part of a right mandibular ramus with broken teeth, and a fragment of a left mandibular ramus with M_2 ; Nos. 1795 and 1794, California Institute of Technology Collection of Vertebrate Paleontology.

Age: Middle Pliocene. *Fauna:* Smiths Valley. *Locality:* Near the western mouth of Wilson Canyon, about twelve miles south-southwest of Yerington, Lyon County, Nevada.

Remarks.—The mandibular ramus of the ground squirrel from Smiths Valley is smaller than that of *C. argonautus* and *C. gidleyi* and is slightly larger than that of *C. lateralis chrysodeirus*. M_2 is wider than long and its dental pattern is that of a ground squirrel with relatively unspecialized dentition such as *Otospermophilus* or *Callospermophilus*. The posterolophid does not continue forward to the parametacoid as was assumed by Wilson (1936: 19), but terminates buccally in a weak entoconid. A mesostylid is present. Except for its large size and relatively greater width, this M_2 is like that of *C. gidleyi*.

These specimens are referable to the genus *Citellus*, as is shown by the proportions of the mandibular ramus and the shape of the teeth, but its subgeneric position is uncertain. It cannot be referred to the subgenus *Citellus*.

Measurements: alveolar length of mandibular tooth row of No. 1795, 9.0; greatest length and width of M_2 of No. 1794, 2.1 and 2.5.

CITELLID sp. Wilson

Citellid sp. Wilson, 1937:33.

Age: Middle Pliocene. *Fauna:* Bartlett Mountain. *Locality:* Near Drewsey, Harney County, Oregon.

Remarks.—This form is mentioned in a faunal list. It is in an undescribed assemblage of specimens in the collection of the California Institute of Technology.

TAMIAS (NEOTAMIAS) ATELES (Hall)

Eutamias ateles Hall, 1930:314, figs. 1, 2; Henshaw, 1942:104.

Type. Worn right M^1 , M^2 , and M^3 ; No. 28521, University of California Museum of Paleontology.

Material referred. No. 28522, slightly worn right M^2 ; No. 28523, slightly worn right M_3 ; No. 35616, slightly worn left M^1 ; University of California Museum of Paleontology.

Age: Upper Miocene. *Fauna:* Barstow. *Locality:* Eleven miles northeast of Hinkley, San Bernardino County, California.

Diagnosis. Teeth small, size about as in *Tamias quadrivittatus inyoensis*; protoconules absent; protoloph not greatly constricted at junction with protocone; metaconules smaller than in existing species of *Neotamias*; mesostyles relatively large; posterointernal part of M_3 large.

Remarks.—The large posterointernal part of M_3 and the absence of protoconules are the outstanding differential features. In Recent *Neotamias* the protoconules are well developed and the protoloph is constricted at their junctions with the protocones. There are no furrows marking the union of the

anterior and posterior cingula with the protocone, as is usual in Recent chipmunks.

The reference of the Barstow specimens to *Neotamias* might lead one to infer that they exhibit marked differences from the subgenus *Tamias*, but such is not so. I have been unable to find significant differences in the dental patterns of the molars of *Neotamias* and *Tamias*. The material is referred to *Neotamias* because of the small size of the molars and also because this genus is represented by numerous western species at the present time. *Tamias ateles* is the only fossil chipmunk known from North America prior to the Pleistocene. Its presence in the Upper Miocene shows the antiquity of the chipmunks in North America.

Measurements: No. 28521: width of M¹, M², and M³, 1.6, 1.6, and 1.6; length of M¹, M², and M³, 1.4, 1.5, and 1.6; No. 28522: length and width of M², 1.5 and 1.8; No. 35616: length and width of M¹, 1.4 and 1.8; No. 28523: length and width of M³, 1.7 and 1.5.

PALAEARCTOMYS Douglass

Diagnosis.—Skull larger than that of other North American sciurids, except *Marmota*. Rostrum massive; cranium markedly flattened and sagittal crest prominent; parietal ridges fuse at level of posterior ends of temporal fossae; two chambers (postpalatine vacuities) open posteriorly below posterior end of hard palate. Incisors large and strong, with many longitudinal striations; upper incisors with two or more distinct grooves on anterior surface; cheek teeth resemble those of *Marmota* but are more brachydont and are smaller in proportion to the size of the skull.

PALAEARCTOMYS MONTANUS Douglass

Palaearctomys montanus Douglass, 1903:183, fig. 23; Matthew, 1909:116.

Type. A skull without the right zygomatic arch, parts of the cranium, and the cheek teeth; nearly complete right and left mandibular rami with worn cheek teeth; and parts of the body skeleton. No. 740, Carnegie Museum Section of Vertebrate Paleontology.

Age: Upper Miocene. *Fauna:* Lower Madison Valley. *Locality:* Madison Valley, probably about five miles north of Logan, Gallatin County, Montana.

Diagnosis. Skull larger and relatively slenderer than that of *P. macrorhinus*. Zygomatic arches slightly convex laterally. Longitudinal ridges on upper incisor coarse; upper incisor relatively narrower and longer than in *P. macrorhinus*. Symphyseal suture of jaw extensive.

Remarks and measurements. See following species

PALAEARCTOMYS MACRORHINUS Douglass

(Pl. 8, figs. a, b)

Palaearctomys macrorhinus Douglass, 1903:184, figs. 24, 25; Matthew, 1909:116.

Type. A skull without the left zygomatic arch and the occipital region; upper incisor, right P⁴, left M¹, M² and M³ present; No. 733, Carnegie Museum Section of Vertebrate Paleontology.

Age: Upper Miocene. *Fauna:* Lower Madison Valley, probably about five miles north of Logan, Gallatin County, Montana.

Diagnosis. Skull robust; smaller and relatively stouter than that of *P. montanus* and *Marmota monax*. Rostrum particularly massive; zygomatic arches markedly convex lat-

erally; longitudinal ridges on upper incisor fine; upper incisor short and heavy; upper diastema long; cheek teeth small.

Remarks.—The skull of *Palaearctomys* resembles that of *Marmota* in general appearance but differs in details, the most significant of which are pointed out in the generic and specific diagnoses. Convergence undoubtedly accounts for many of the similarities between these two genera, but it is evident, as shown by Douglass, that *Palaearctomys* is more closely related to *Marmota* than to any other existing genus of sciurids. However, it differs from *Marmota* in characters which suggest that it diverged from the marmot line of descent at an early stage. These differences are: greatly reduced P^3 , more dorsal position and slitlike shape of the infraorbital foramina, relatively larger incisors and smaller cheek teeth, and the presence of postpalatine vacuities. *Palaearctomys* has retained characters which may have been present in the forms ancestral to it and *Marmota*, such as the large grooved incisors, mesodont cheek teeth, distinct entoconids, broad postorbital processes, small orbits, and large condyloid and coronoid processes. The lower cheek teeth (*P. montanus*) are heavily worn and the dental pattern is not discernible. In shape they resemble the cheek teeth of *Arctomyoides arctomyoides* more closely than they resemble those of *Marmota*, as would be expected in view of the relative ages of these genera, but they are more hypsodont and are relatively broader.

Measurements: No. 740, *P. montanus*, and No. 733, *P. macrorhinus*: occipitonasal length of skull, 101.4,; length from most anterior point of premaxilla to posterior end of zygomatic arch, 73.0, 63.7; greatest zygomatic breadth (determined by doubling one-half the width), 69.4, 61.6; distance from upper incisor at alveolus to anterior border of posterior palatine vacuities, 42.2, 37.1; depth of rostrum at incisive foramina, 25.7, 21.5; greatest width of rostrum at level of incisive foramina, 21.3, 23.0; depth of upper incisor at alveolus, 7.2, 7.0; width of upper incisor at alveolus, 4.6, 5.1. No. 740: length of mandibular ramus from anterodorsal margin of tip of condyloid process, 60.9; depth of mandibular ramus through diastemal portion, 14.1; depth of mandibular ramus below M_1 , 16.5; depth and width of lower incisor at alveolus, 7.2, 3.4; length of mandibular tooth, row, 15.3; greatest length of P_4 , M_1 , M_2 , and M_3 , 3.6, 3.5, 3.7, and 4.4; greatest width of P_4 , M_1 , M_2 and M_3 , 3.3, 3.9, 4.6 and 4.1. No. 733: length of maxillary tooth row, 15.7; greatest length of P_4 , M^1 , M^2 and M^3 , 3.5, 3.9, 3.9 and 4.1; greatest width of P_4 , M^1 , M^2 and M^3 , 3.8, 4.3, 4.4 and 4.1.

PALAEARCTOMYS VETUS (Marsh)

Arctomys vetus Marsh, 1871:121; Trouessart, 1897:445; Matthew, 1899:66; Hay, 1902:720.

Arctomys vitus King, 1878:430.

Palaearctomys vetus Matthew, 1909:116.

Type. No. VP10323, Yale Peabody Museum. Not seen by the author.

Age: Miocene or Pliocene, exact age not known. Fauna: Faunal stage not known.

Locality: "On the Loup Fork, in Northern Nebraska."

Remarks.—I have not had an opportunity to study *Palaearctomys vetus* and little definite information concerning this species is available in the literature. Marsh (*loc. cit.*) states: "A small species of the genus *Arctomys*, represented by a nearly perfect lower jaw, and other remains, was discovered during our explorations on the Loup Fork River. This species was only about one-third the size of the modern *Arctomys monax* Gmelin, and may at once be

distinguished from that rodent by the lower incisors, which have on the anterior surface a shallow median groove. The molar teeth of the lower jaw have essentially the same composition as those of the larger species."

Arctomyoides, new genus

Type.—*Sciurus arctomyoides* Douglass; No. 741, Carnegie Museum Section of Vertebrate Paleontology.

Diagnosis.—Mandibular ramus in front of P_4 small in comparison with greatly enlarged posterior portion; diastemal region relatively shallower, longer, and broader than in *Sciurus*, proportions similar to those of *Marmota*; masseteric fossa large, located dorsally so that its anterior end almost touches alveolar border below M_1 ; coronoid and condyloid processes well developed as in Recent terrestrial sciurids; anterior end of coronoid process merges with alveolar border below M_2 . Upper incisor stout, finely crenulated, with a distinct median longitudinal groove; P^3 small; parastyle on P^4 large; mesostyles, mesostylids, and distinct mesoconids and entoconids present on cheek teeth.

ARCTOMYOIDES ARCTOMYOIDES (Douglass)

(Pl. 8, fig. f)

Sciurus arctomyoides Douglass, 1903:181, fig. 22; Trouessart, 1904:318; Matthew, 1909:116; Gazin, 1932:58.

Type. Upper incisors in fragments of the premaxillae; the right P^3 , P^4 , and M^1 in a fragment of the maxilla; a nearly complete left mandibular ramus with all of the teeth; and a part of a right mandibular ramus with lower incisor. No. 741, Carnegie Museum Section of Vertebrate Paleontology.

Age: Upper Miocene. *Fauna*: Lower Madison Valley. *Locality*: Madison Valley, probably about five miles north of Logan, Gallatin County, Montana.

Diagnosis. Mandibular ramus slightly larger than that of *Cynomys l. ludovicianus*, larger than that of any North American species of *Sciurus* and smaller than the rami of *Marmota* and *Palaeosciurus*. Masseteric fossa broadly rounded anteriorly; terminates below posterior margin of P_4 .

Remarks.—The upper incisors are flat laterally and medially and slightly convex anteriorly. At the alveolus the width is 65 percent of the depth. The anterior surface bears a shallow, median longitudinal groove and is finely crenulated. P^3 is a minute cone. P^4 is several times as large as P^3 and one half as large as M^1 . The anterior cingulum and parastyle of P^4 are large and the tooth is consequently triangular in occlusal outline, and its length along the labial margin is greater than the width. M^1 is broadly triangular in occlusal view, is wider than long, and its labial length is little greater than its buccal length. The parastyle and anterior cingulum are large. On both P^4 and M^1 the protoconids and metaconids converge toward the protocone, are moderately high, and are constricted near their union with the protocones. The posterior cingula are small, and the mesostyles are well developed.

The lower incisors are narrower than the upper incisors and lack the longitudinal groove. DP_4 is present; the protoconid connects the bases of the protoconid and parametaconid and, with the metalophid, incloses a small valley; the entoconid is small, the talonid basin is deep, the ectolophid is near-

ly marginal, and a mesoconid is present. M_1 and M_2 are rhomboidal in occlusal outline and M_3 is slightly longer than wide. The lower molars are moderately high crowned, the protolophids and posterolophids are well developed, and the talonid basins are deep. The metalophids extend mediad a short distance from the protoconid but do not reach the parametaconid. The labial margins of the molars slant inwardly, the ectolophids are situated well in from the labial margins, the talonid basins are reduced in width, and the grooves between the protoconids and hypoconids are large. Small ectostylids and large mesoconids and mesostylids are present. The posterolophids are crescentic.

The diastemal part of the mandible is long and rather shallow, and the mental foramen is situated in the middle of its lateral surface. The masseteric fossa ends below P_4 , and its ventral crest is strong. The dorsal margin of the vertical ramus slants posterodorsad past the posterior margin of M_2 . The dorsal margin of the anterior end of the ramus, the alveolar border, and the dorsal surface of the condyloid process are on the same plane.

In the original description of *Sciurus arctomyoides* Douglass (1903:182) says that "the teeth are intermediate between those of *Sciurus* and *Arctomys*, rather more resembling some species of the former." Comparison of the fossils with Recent sciurids shows that the first part of this statement is true and that the latter part is incorrect. *S. arctomyoides* resembles Recent *Sciurus* in the small size of P^3 and the presence of large mesoconids and small entoconids. The latter feature gives M_1 and M_2 a rhomboidal shape as in *Sciurus*. Features of difference from *Sciurus*, which are at the same time features in agreement with Recent terrestrial forms, particularly *Marmota*, are: enlarged parastyles, protocones of P^4 and M^1 small and the teeth consequently triangular in occlusal outline, protolophs and metalophs convergent toward the protocones rather than parallel, ectolophids elevated and situated well in from the margins of the molars, talonid basins deep and longer than wide, posterolophids crescentic, diastemal portion of mandibular ramus long and shallow and its anterodorsal border as high as the alveolar border, and the dorsal surface of the condyloid process is level with the mandibular tooth row. The shape of the incisors and the height of the crowns of the cheek teeth are intermediate between *Sciurus* and *Marmota*, but are more like the former.

The paleontological evidence leaves little doubt that the teeth of *Sciurus* are more primitive than are the teeth of other Recent Nearctic sciurids. The Madison Valley specimens had diverged too far from the primitive type by the Upper Miocene to be placed in the genus *Sciurus* and, as far as the available material permits one to ascertain, represents a line of descent leading toward the marmots. The teeth had become mesodont but had not yet attained the semi-hypsodonty of *Marmota*. The small size of P^3 seems to be a primitive feature, since it is small in all pre-Pleistocene fossil sciurids. It appears to have increased in size in correlation with the higher and broader molar teeth. The dental pattern does not differ fundamentally from that of *Marmota*. Since the retention of this form in the genus *Sciurus* gives a false impression of its relationships, the name *Arctomyoides arctomyoides* is proposed as a substitute for *Sciurus arctomyoides*.

Measurements: Length of diastema of mandibular ramus, 12.5; depth of mandibular

ramus through mental foramen, 9.4; depth of ramus below anterior end of P_4 , 11.0; depth and width of upper incisor at alveolus, 4.0, 2.6; diameter of P_3 , 1.2; greatest length and width of P_4 and M_1 , 3.3 and 3.2, 3.9 and 4.4; alveolar length of mandibular tooth row, 15.4; greatest length of P_4 , M_1 , M_2 and M_3 , 3.3, 3.9, 4.1, and 4.3; greatest width of P_4 , M_1 , M_2 , and M_3 , 3.1, 4.1, 4.4, and 4.1.

MARMOTA NEVADENSIS (L. Kellogg)

Arctomys nevadensis L. Kellogg, 1910:422, figs. 1a, 1b, 2; Merriam, 1911:211, 214, 253; Merriam, 1917:429.

Marmota nevadensis Wilson, 1937:34.

Type. The anterior part of a left mandibular ramus with a broken lower incisor; P_4 and M_1 intact. No. 12506, University of California Museum of Paleontology.

Material referred. A right P_4 , half of a left P_4 , and a right lower incisor in a fragment of the mandibular ramus; No. 12544, University of California Museum of Paleontology.

Age: Middle Pliocene. *Fauna:* Thousand Creek. *Locality:* Thousand Creek, Humboldt County, Nevada.

Diagnosis. Ramus larger and relatively stouter than that of other Nearctic species of *Marmota*. Masseteric fossa not clearly delimited anteriorly and terminates below M_1 . P_4 and M_1 nearly rhomboidal in occlusal view; protoconulid on P_4 minute and closely appressed to protoconid.

Remarks.—The mandibular ramus of *Marmota nevadensis* is massive, particularly at the anterior end of the masseteric fossa. The mental foramen is situated ventral and slightly anterior to P_4 . The protolophid on P_4 is a ridge extending ventromedial from the protoconid to the base of parametacoid. It bears a small protoconulid near the protoconid. In Recent *Marmota* the protolophid is not present as a distinct crest and the protoconulid is a moderately large cusp situated low in the middle of the anterior face of the P_4 . The ectolophids are prominent as in Recent *Marmota*. The posterolophid on P_4 bears several small cusps and on M_1 appears to have had a small hypoconulid. Well developed mesostylids and indistinct mesoconids are present. An ectostylid occurs on P_4 . The floors of the talonid basins are rugose. P_4 is not as large as M_1 .

The dental pattern and the shape of the mandibular ramus show that *M. nevadensis* is closely related to Recent species of *Marmota*. The teeth represent a stage of development between that of a form like *Arctomyoides arctomyoides* and Recent *Marmota*. Kellogg (1910:425) states that this species is nearest to *M. primigenia* from the Pleistocene of Paris.

Measurements: No. 12506: length of diastema, 19.1; width of mandibular ramus over mental foramen, 15.2; distance from base of P_4 to mental foramen, 11.2; depth and width of lower incisor, 6.4 and 4.1; median length of P_4 and M_1 , 5.8 and 6.3; width of trigonid of P_4 and M_1 , 5.1 and 6.4; width of talonid of P_4 and M_1 , 5.9 and 6.9. No. 12544: depth and width of lower incisor, 6.9 and 4.6; length of P_4 and width of trigonid, 7.4 and 6.1.

MARMOTA MINOR (L. Kellogg)

Arctomys minor L. Kellogg, 1910:425, figs. 3-7; Merriam, 1911:211, 213, 214, 253; Merriam, 1917:429.

Marmota minor Wilson, 1937:34.

Type. Part of a left maxilla with P₃ and P₄; part of a right mandibular ramus; parts of upper and lower incisors; right M₂ and M₃ in a fragment of the maxilla; M₂ and M₃ in a fragment of the left mandibular ramus; and right P₄, M₁ and M₂. No. 12538, University of California Museum of Paleontology.

Age: Middle Pliocene. *Fauna:* Thousand Creek. *Locality:* Thousand Creek, Humboldt County, Nevada.

Diagnosis. Smaller than *Marmota flaviventer sierrae*. Parametaconid on P₄ slender and slightly higher than protoconid, the two connected by a complete but low protocholid with a well developed median protoconulid; the incisors and P₄ large in proportion to the other teeth; lower molars wider than long.

Remarks.—P₄ and P₃ differ from Recent *Marmota* only in size. P₄ is slightly larger than M₁, thus resembling *M. flaviventer*. The lower molars are relatively wider than those of *M. nevadensis* but are not as compressed antero-posteriorly as in existing marmots. The detailed differences between this species and *M. monax* and *M. flaviventer* have been discussed by Kellogg (1910:426-427).

Measurements: Depth and width of upper incisor, 4.2 and 3.3; length of M₂ and M₃, 3.4 and 4.2; width of M₂ and M₃, 4.1 and 4.1; depth and width of lower incisor, 4.1 and 2.7; width of trigonid and length of P₄, 3.4 and 4.2.

MARMOTA sp. Gazin

Marmot sp. Gazin, 1936:285; Schultz, 1937:84; Wilson, 1937:38.

Age: Upper Pliocene. *Fauna:* Hagerman. *Locality:* On Snake River across from Hagerman, Twin Falls County, Idaho.

Remarks. A marmot has been reported in the fauna from the Hagerman deposits.

CYNOMYS sp. Matthew

Cynomys sp. Matthew, 1899:66; Matthew, 1909:116; Merriam, 1917:438.

Age: Miocene or Pliocene, exact age not known. *Fauna:* Republican River of Nebraska.

Remarks: A species of *Cynomys* from Nebraska was first reported by Matthew (1899:66) in a list of Tertiary mammals and has been subsequently mentioned in faunal lists. The specimens have not been described or figured.

CYNOMYS sp. Hibbard

Cynomys sp. Hibbard, 1937:244.

Age: Upper Pliocene. *Fauna:* Rexroad. *Locality:* Meade County, Kansas.

Remarks. Hibbard states: "The genus *Cynomys* is represented by three molars, No. 3928, larger than the molars of *Cynomys l. ludovicianus*." These molars were not seen by the author.

Discussion

If it were possible to determine the ancestral prototype of the Sciuridae, the problem of evolution within the family would be greatly simplified. Unfortunately, there are few fossil sciurids from deposits older than the Upper Miocene, and the family probably originated in the Eocene. There is little doubt that the family Sciuridae has been derived from the protogomorphs, as suggested by Matthew (1910) and others, and that the family Paramyidae is more closely related to the Sciuridae than is any other family of rodents. This

assumption is based on the similarity in the dental pattern and structure of the skull of *Paramys* and sciurids. Intergradation between the Paramyidae and Sciuridae cannot be proven at this time, although the mandibular rami of the squirrels of the Lower Miocene are intermediate in certain features, and the skulls of the Upper Miocene sciurids have paramyid characters. Also, if negative evidence be allowed, no other family of primitive rodents possesses features which appear to be possibly ancestral to the Sciuridae. Assuming that the Paramyidae (*Paramys*) do represent the prototype, the evolutionary trends in some of the phylogenetically significant characters of the Sciuridae can be outlined.

The zygomatic structure and the dentition are the most significant features in the determination of the relationships of the sciurids. Other features of the skull which have undergone divergent changes in time are: the proportions of the rostrum, the shape and position of the infraorbital foramen, the proportions of the cranium, the proportions of the mandible, and the form of the masseteric fossa and of the processes of the mandible.

Dentition.—The following described concept of the primitive dentition in squirrels has been arrived at by comparing the dentitions of the fossil sciurids and paramyids and by taking into account the features common to existing

sciurids. The primitive dental formula was $\frac{1-0-2-3}{1-0-1-3}$. The upper incisors were

oval in cross section and the depth of each was about twice as great as its width. The lower incisors were also stout but were more flattened than the upper ones. P^3 was much smaller than P^4 , single-rooted, and of but slight use to the animal. P^4 was somewhat molariform, the parastyle and anterior cingulum were small, the protocone was smaller than that of M^1 , and the tooth was triangular in occlusal outline. The upper molars were brachydont and were progressively larger from M^1 through M^3 . M^1 and M^2 were quadrate in occlusal outline, the protocones were nearly as broad as the labial margins, and the cingula were nearly parallel. On the upper cheek teeth, excepting P^3 , the low protoloph and metalophs were convergent toward the protocones, metaconules were present and were separated from the protocones by sulci, mesostyles were present, and hypocones were absent. The metacone on M^3 was much larger than on any other cheek tooth and was situated posteriorly rather than labially; M^3 was consequently nearly triangular in occlusal view and was slightly longer than wide. The lower cheek teeth were brachydont and on each the talonid was nearly as high as the trigonid, the ectolophid was low and submarginal, a large mesoconid and a large mesostylid were present, and the entoconid was a distinct cusp situated at the lingual end of the crescentic posterolophid. The protoconid and parametaconid on P_4 were close together. The protolophid was small, and P_4 was not molariform. Both M_1 and M_2 were nearly rhomboidal in occlusal outline. M_3 was little larger than M_2 , the hypoconid was larger and located more posteriorly than that on the other lower molars, and M_3 was longer than wide.

The incisors of Miocene squirrels retained the primitive condition, insofar as determinable except in *Palaeartomys*, in which the cheek teeth were rela-

tively small and the incisors were correspondingly enlarged. In the Pliocene the incisors became more compressed and relatively deeper anteroposteriorly in the tree squirrels and remained broad in comparison with the depth that obtained in other squirrels. The incisors of Recent genera exhibit the same general form as these teeth have in the corresponding Pliocene genera in all instances where comparable material is available.

As compared with the primitive crown height, the cheek teeth were slightly higher crowned in the Upper Miocene genera *Palaearctomys*, *Arctomyoides*, *Protospermophilus*, and *Citellus*. The cheek teeth of tree squirrels have remained brachydont. The Middle and Upper Pliocene species of *Citellus* have mesodont cheek teeth, as have the Recent ground squirrels except in the subgenus *Citellus*. A semihypsodont condition has been attained in *Cynomys*, *Marmota*, and the subgenus *Citellus*.

P³ was small in the Miocene sciurids, as it was in the Paramyidae, but since the Miocene P³ has undergone regressive changes in some squirrels and has become larger in others. P⁴ is somewhat molariform in all sciurids but is rarely as large as M¹. The primitive quadrate shape of M¹ and M² has been retained in *Sciurus*, *Tamiasciurus*, and *Glaucomys*. In the Upper Miocene the protocones on M¹ and M² had been reduced in size and the occlusal surfaces were subquadrate or triangular in the terrestrial squirrels and chipmunks. Metaconules are present on the cheek teeth of all sciurids except the post-Miocene tree squirrels, in which they are usually absent and are small when present. Mesostyles are present in all the upper molars known of fossil sciurids. Among Recent groups they are absent in *Glaucomys* and are either absent or small in most of the terrestrial squirrels.

The P₄ was not molariform in Miocene and Lower Pliocene sciurids, but it had become somewhat molariform in the Middle Pliocene marmots. Among Recent Nearctic sciurids it is truly molariform in *Cynomys* and the subgenus *Citellus* and is nearly molariform in *Marmota*. With the increase in the height of the crowns of the lower molars there has been a tendency toward an inward movement of the ectolophids and a consequent reduction in size of the talonid basins. In these features, the primitive condition has been retained in tree squirrels and the most highly specialized condition is found in *Cynomys*, *Marmota*, and the subgenus *Citellus*. In tree and flying squirrels the entoconid region is well developed; in the other genera of sciurids the entoconid is minute and this region of the molar is reduced in size.

Skull.—The rostrum of most of the Miocene squirrels was massive. In Recent *Sciurus* it is relatively as deep as in the Miocene forms, but it is not as broad and is consequently less massive. The primitive massive condition of the rostrum is characteristic of *Marmota*. In *Citellus ridgwayi* the rostrum was shallow in comparison with that of *Sciurus* and thus *C. ridgwayi* resembled modern ground squirrels. *Protospermophilus quatalensis* had a massive rostrum and was more primitive in this respect than the older *C. ridgwayi* and *P. tephros*.

The zygomatic plate in the Miocene sciurids, except in *Palaearctomys*, ended posteroventrally opposite the posterior end of P₄, and in Recent genera

it ends either opposite P_4 or M_1 . In *Palaeartomys* the zygomatic plate ended opposite M_1 . The zygomatic plates were smaller in Miocene forms than they are in Recent members of the same phyletic line.

The infraorbital foramen was probably small and round in the primitive sciurids as it was in the protrogomorphs. In *Palaeartomys* and *Sciurus* it is a narrow slit; it is an oval or subtriangular opening in terrestrial squirrels, chipmunks, and flying squirrels. In the chipmunks the infraorbital foramen pierces the zygomatic plate and an infraorbital canal is absent.

The cranium of Miocene squirrels was flattened dorsoventrally as it was in the protrogomorphs. In Recent tree and flying squirrels it is greatly inflated and the dorsal profile of the skull is consequently markedly convex. In the other North American genera of sciurids, with the possible exception of *Mar-mota*, the cranium is more inflated than it was in the Miocene forms but is relatively more depressed than in tree and flying squirrels.

The mandibles of *S. tecuensis*, *S. vortmani*, and *S. balloviensis* are intermediate in structure between those of *Paramys* and Upper Miocene squirrels. In the Upper Miocene the characteristic features in the mandibles of the phyletic lines of the tree squirrel and terrestrial squirrel were established. In *S. tecuensis*, from the Lower Miocene, the masseteric fossa was deep and ended anteriorly below the protoconid of M_1 . The fossa also ended posterior to the level of P_4 in *S. vortmani* and *S. balloviensis*. In the *Paramyidae* the masseteric fossa terminates anteriorly below M_2 , whereas it ends below P_4 in the Upper Miocene, Pliocene, Pleistocene, and Recent sciurids. It is evident that there has been a forward movement of the masseter muscle from its primitive position on the mandible, along with its movement forward from the zygomatic arch to the zygomatic plate.

Classification of Nearctic Sciuridae

A comparative account of the external features, osteology, myology, and paleontology of Nearctic sciurids has been presented in the foregoing pages. The problem now is to evaluate the characters which are judged to be phylogenetically significant.

Rodents differ from other mammals primarily because they gnaw. The gnawing has indirectly induced changes in the incisor teeth and in the masticatory muscles. With these changes have come correlative modifications in the parts of the skull associated with the incisors and the masticatory muscles. The muscles used most in chewing are those situated nearest the incisors, because the mandible is situated posteriorly when it is at rest and has to be brought forward into position for chewing, and because the mechanical advantage of the forwardly placed muscles is greater than that of the muscles situated farther posteriorly. The principal masticatory muscles in the order of increasing distance from the incisors are the masseter, the pterygoid, and the temporal. Consequently, the masseter muscles of rodents have been modified the most, and the temporal muscles least.

The masseter primitively originates along the zygomatic arch and anteriorly as far as the region of the infraorbital foramen and inserts over the outer

surface of the posterior half of the mandible. In rodents the masseter is divisible into lateral and medial parts, and these parts have developed in various ways. The main subdivisions of rodents, usually called suborders or superfamilies, are primarily based on the variable development of these parts and on the resultant structural changes in the skull. In the Sciuridae the lateral part has differentiated into the masseter superficialis and the masseter lateralis. The superficial part originates on the masseteric tubercle below the infraorbital foramen and has a subordinate role in shaping the zygomaseteric structure. The anterior part of the masseter lateralis has extended its origin forward over the infraorbital foramen and the anterior surface of the zygomatic arch, and it has taken the major part in shaping the zygomaseteric structure. The posterior part of the masseter lateralis and the medial part of the masseter have retained their primitive attachments. This basic sciurid zygomaseteric plan has undergone modification and in Nearctic Sciuridae there are three subtypes. One subtype is peculiar to the flying squirrels, a second subtype to tree squirrels, and a third to the chipmunks and terrestrial squirrels (see pages 274 and 275). If my conclusions concerning the phylogenetic significance of the zygomaseteric structure of rodents in general are valid, it follows that this structure and the correlated structure of the mandible take precedence over other features in phylogenetic importance and that the three groups mentioned above are natural. Although my study is restricted to the Nearctic squirrels, it is perhaps significant that the squirrels of the world, as known by the figures available in Ellerman's (1940) treatise, fall into these same three categories of zygomaseteric structure. In comparison with the changes in the parts associated with the masseter muscle, the changes in the parts of the skull which are associated with the pterygoid and temporal muscles are small and, because they are less intimately connected with gnawing, are of subordinate phylogenetic importance.

The configuration of the teeth ranks next in phylogenetic significance to the zygomaseteric structure and the structure of the parts of the mandible correlated with it. The height of the crown, the occlusal outline, the degree of convergence of the protoloph and metaloph toward the protocone, and the position of the ectolophid have greater suprageneric significance than the other features of the dentition. This is true because evolutionary trends are apparent in these characters, which trends coincide with the phyletic lines indicated by the zygomaseteric structure, and because these characters exhibit only minor variations within the suprageneric group of squirrels. Such details of the teeth as the presence or absence of subsidiary cusps, the union or separation of the protocone and metaloph, the sizes of the cingula, and the shape of the incisors are of secondary importance because they vary supraspecifically and in some instances they vary specifically.

P³ merits special consideration. Two of the premolars are absent from each side of the upper jaw of all rodents except *Heliophobius*, in which P² is present (Ellerman, 1940:80). P³ and P⁴ have disappeared in some rodents, and there is a tendency toward the loss of these teeth in squirrels. In the Sciuridae P³ varies in size from a large, functional tooth in *Cynomys* to a small, peglike tooth in *Neotamias*, in which it is occasionally absent (see table

1, page 286). It is absent in the subgenus *Tamias* and in *Sciurus niger* and is small in the other species of *Sciurus* examined. P^3 is small or absent in *Tamiasciurus*. In view of these facts I conclude that the absence of P^3 is merely the final phase of an evolutionary trend and has no supraspecific significance. P_3 is absent in sciurids.

The brain is considered a conservative structure because it is not as greatly affected by the indirect molding influence of the environment as are the skeletal and muscular systems. Consequently, the features of the cranium which appear to be directly correlated with the development of the parts of the brain are assumed to be paleotelic. Absolute proof of the correlation between the structure of the parts of the cranium and the development of the parts of the brain must await a comparative study of the brains of sciurids, which has not been made. Features which appear to be so correlated and which exhibit supraspecific variation are the size of the anterior cranial fossa, the width of the skull dorsal to the anterior cranial fossa, the postorbital constriction, and the degree of inflation of the cranium. The position of the premaxillary-maxillary suture is also a paleotelic character.

The presence or absence of cheek pouches in squirrels has broad evolutionary significance. It is not reasonable to assume that the cheek pouches in any two groups of squirrels have had an independent origin, because the pouches have the same relations to the complex extrinsic musculature in all sciurids with pouches.

The most significant characters for determining the relationships of the Nearctic Sciuridae are the zygomaseteric structure and the structure of the mandible correlated with it, the position of the premaxillary-maxillary suture, the characters of the cranium directly correlated with the form of the parts of the brain, certain features of the dentition, and the presence or absence of cheek pouches. As determined by these characters there are three main groups or phyletic lines of squirrels in North America: terrestrial squirrels and chipmunks, tree squirrels, and flying squirrels. The present study is too restricted to justify the designation of these three groups as subfamilies, although they may merit this designation. Cenotelic characters are included in the following characterizations of the supraspecific categories, but the categories have been established on the basis of the paleotelic characters.

Terrestrial Squirrel and Chipmunk Division

Characters.—The zygomaseteric structure is as follows: infraorbital foramen oval, vertical, and situated near P^3 ; masseteric tubercle situated ventral to infraorbital foramen; fossa in zygomatic plate for origin of anterior part of masseter lateralis narrow, long, and convex; anterodorsal margin of zygomatic plate terminates at premaxillary-maxillary suture; zygomatic plate tilted upward at an angle of 50° or less to basicranial axis; dorsal head of maxillo-nasalis muscle arises on dorsolateral margin of zygomatic plate and this margin is raised to form a crest; internal face of zygoma is turned dorsomedially because zygoma is twisted outward; zygomata convergent anteriorly; entire outer surface of zygoma occupied by fossa for origin of posterior part of masseter lateralis. Premaxillary-maxillary suture crosses anterior tip of zygomatic

plate, runs ventrad well in front of masseteric tubercle, and passes antieriad to the incisive foramen only after attaining the ventral surface of the rostrum. In comparison with tree squirrels anterior cranial fossa is small, interorbital region is narrow, and cranium is not greatly inflated. Diastemal part of mandible relatively long and shallow; anterior end of mandible level with or above level of alveolar border; coronoid process of medium or large size; base of condyloid process narrow and dorsal margin of process on level with or only slightly above level of mandibular tooth row; angular process not rounded, pointed at posterodorsal angle (see figs. 29-42). Incisor teeth broad in comparison with anteroposterior depth; on M^1 and M^2 protocone narrower than labial margin, protoloph and metaloph converge toward protocone, and occlusal outline is triangular or subquadrate (see table 1); on M_1 and M_2 hypoconid not larger than protoconid, entoconid indistinct, entoconid region rounded, and postero-lophid runs from hypoconid toward parametaconid in an even arc. Cheek pouches present.

Terrestrial squirrels and chipmunks are further characterized by the following features: jugal bone without frontal processes; seven true ribs; manubrium pentagonal or quadrilateral in outline and blunt anteriorly; metacromion, acromion, and coracoid process of scapula distinctively shaped (see page 296); part of second sacral vertebra included in pelvic articulation; maxillonasalis muscle Y-shaped; platysma 4 attaches to metacromion.

Remarks.—Several fossil terrestrial squirrels and one fossil chipmunk are known from the Upper Miocene. The tree squirrels are known by Lower Miocene and Lower Pliocene fossils. The fossils record thus corroborates the conclusion derived from anatomical studies that the phyletic line of the terrestrial squirrels and chipmunks and that of the tree squirrels diverged early in the evolutionary history of the Sciuridae and proves the time of divergence to have been prior to the Upper Miocene. The phyletic line of the chipmunks diverged from that of the terrestrial squirrels prior to or in the Upper Miocene.

CHIPMUNK SECTION

Genus *TAMIAS*

Type species.—*Sciurus striatus* Linnaeus.

Characters.—Zygomatic plate slants upward at an angle of about 45° to basicranial axis and is more nearly horizontal than in other sciurids; in correlation with this the zygoma is less concave dorsally than in other squirrels, infraorbital foramen pierces zygomatic plate, and infraorbital canal is absent. Infraorbital foramen relatively larger, probably in correlation with origin of ventral head of maxillonasalis muscle (see page 314), and more nearly circular than in other sciurids. Notches in zygomatic plates opposite P^4 or occasionally opposite anterior edge of M^1 ; width of plates between zygomatic notches and infraorbital foramina correspondingly narrow. Anterior cranial fossa larger than that in terrestrial sciurids, except *Otospermophilus* and *Callospermophilus*; interorbital region correspondingly broad. Cranium narrow, slightly inflated,

and smoothly rounded. Dorsal outline of skull less convex than in other squirrels except *Marmota*. Cheek teeth low-crowned (see table 1); ectolophids low and submarginal; prominent mesoconid present on M_1 and M_2 . Form of baculum distinctive (see page 306).

The following characters are cenotelic or are of doubtful status: color pattern of light and dark bands on head and body; process absent at anterior end of fossa on zygoma for origin of posterior part of masseter lateralis (parallels *Ammospermophilus*); supraorbital notches near plane of zygomatic notches in subgenera *Tamias* and *Neotamias*; coronoid process of mandible of medium size (parallels *Ammospermophilus* and *Xerospermophilus*); angular process ends well in front of level of tip of condyloid process; upper incisors sharply curved (parallels *Ictidomys*, *Xerospermophilus*, and *Ammospermophilus*); enameled surfaces of incisors usually longitudinally grooved (parallels *Marmota*); fossa on scapula for teres major short and deep; pubic symphysis short; cheek pouches large; atlantoscaphularis dorsalis muscle present.

Primitive characters which are retained in chipmunks and which have changed or are generically variable in terrestrial squirrels are: pytergyoid fossa narrow; lateral pterygoid plate rudimentary; P^4 not molariform (see page 287); mesostyles present on M^1 and M^2 ; metalophs complete on M^1 and M^2 (retained in some terrestrial sciurids, see table 1); M^3 slightly or no larger than M^2 ; sacrum comprises three vertebrae; clavobrachialis muscle absent. All of these characters are retained in tree squirrels and most of them are present in flying squirrels. The characters are judged to be primitive because they occur in different phyletic lines or represent an unspecialized condition.

Chipmunks resemble tree squirrels and differ from terrestrial squirrels in the following cenotelic features: shape of claws, shape of ears, digits in order of increasing length 1-5-2-3-4, zygomatic arches closely appressed and squamosal roots slant anteriorly (also *Ammospermophilus*), sagittal ridge on ventral surface of second sacral vertebra prominent, fossa on scapula for teres major a deep groove (see page 296), on subscapular ridge present, shape of os coxae (see page 301), and relative lengths of bones of limbs (see table 2).

Subgenus TAMIAS

(Figs. 11, 25, 39; Pl. 2, figs. f, g)

The color pattern consists of five dark and four light stripes alternating on the dorsal area; the two light stripes bordering the median dark stripe are about twice as wide as the median stripe. The zygomatic notch is opposite the posterior part of P^4 or the anterior edge of M^1 , the longitudinal grooves on the incisors are faint or occasionally absent, and P^3 is absent. Compared with *Neotamias* the rostrum is relatively longer, and less constricted at the base, the supraorbital notches are further forward in relation to the plane of the zygomatic notches, the postorbital processes are stouter, the palate is relatively longer, the tympanic bullae are relatively smaller.

Subgenus NEOTAMIAS

(Figs. 10, 24, 38; Pl. 2, figs. d, e)

Type species.—*Tamias asiaticus merriami* Allen [= *Tamias merriami* Allen].

Characters.—The color pattern consists of five dark and four alternating dorsal stripes of approximately equal width. The zygomatic notch is opposite the middle or anterior part of P⁴, the longitudinal grooves on the incisors are distinct, and P³ is present. Other differences from the subgenus *Tamias* are given in the discussion of that group.

Remarks.—The Nearctic chipmunks are usually placed in two genera: *Tamias* and *Eutamias*. *Tamias* was proposed by Illiger (1811:83). Trouessart proposed the subgenus *Eutamias*, distinguished from the subgenus *Tamias* by the presence of two premolars in each maxilla rather than one, for squirrels now assigned to *Eutamias*, *Ammospermophilus*, and *Callospermophilus*. C. H. Merriam (1892:27) removed *Ammospermophilus* from this group. *Callospermophilus* was later removed from the group by C. H. Merriam (1897:189), and *Eutamias* was given generic rank. Merriam did not characterize the genus or give reasons for his action. A. H. Howell (1929:26) divided the genus *Eutamias* into two subgenera: *Eutamias* for the Asiatic chipmunks and *Neotamias* for the chipmunks of western North America. He placed the chipmunks of eastern North America in the genus *Tamias*. Ellerman (1940:426) placed all of the chipmunks in the genus *Tamias* and recognized three subgenera. I am convinced that Ellerman's interpretation of the relationships of the chipmunks is correct.

The presence or absence of P³ appears to have been considered the most significant difference between the genera *Tamias* and *Eutamias*. This character is of significance only in distinguishing between species of squirrels (see page 368). The other differences between the eastern and western chipmunks do not appear to be of sufficient phylogenetic importance to warrant the retention of the two groups as genera.

TERRESTRIAL SQUIRREL SECTION

Characters.—The characters which distinguish the terrestrial squirrels from the chipmunks are: zygomatic plate inclined upward at an angle of about 50° to basicranial axis; infraorbital foramen relatively small, oval or subtriangular in shape, and not piercing zygomatic plate; infraorbital canal present; notches in zygomatic plates opposite M1 in Recent forms; width of plates between zygomatic notches and infraorbital foramina correspondingly broader than in chipmunks; anterior cranial fossa of medium or small size, not as large as in tree and flying squirrels; cranium relatively deeper than in chipmunks; ectolophids prominent and situated well in from labial margins of cheek teeth; mesoconids absent except in *Arctomyoides*; baculum of distinctive type (see page 306).

The following characters are cenotelic or are of doubtful significance: ears and claws of distinctive form (see pages 261 and 262), digits in order of in-

creasing length 1-5-2-4-3, supraorbital notches or foramina situated well anterior to plane of zygomatic notches, pterygoid fossa broad and lateral pterygoid plate prominent, teres major fossa of scapula small and ungrooved, two or three subscapular ridges present, and os coxae of distinctive form (see page 301). Fossil members of this section possess the features mentioned in this and the preceding paragraph insofar as the material permits one to determine.

Remarks.—The phyletic line of the marmots separated from that of the other terrestrial squirrels before the radiation of the other forms began. *Arctomyoides arctomyoides* from the Upper Miocene appears to represent the marmot line. The ground squirrel-prairie dog line is represented by a number of Upper Miocene fossils. The degree of morphological differences between the marmots and the other terrestrial squirrels provides additional evidence of the early separation of these two phyletic lines.

MARMOT SUPRAGENERIC GROUP

Genus ARCTOMYOIDES

(Pl. 8, fig. f)

Type species.—*Sciurus arctomyoides* Douglass.

Arctomyoides is known only from one specimen of Upper Miocene age. Its characters and relationships are discussed on pages 360 and 362.

Genus PALAEARCTOMYS

(Pl. 8, figs. a, b)

Type species.—*Palaearctomys montanus* Douglass.

Palaearctomys is known from two Upper Miocene and one Lower Pliocene species. The characters and relationships of the genus are discussed on pages 359-361.

Genus MARMOTA

(Figs. 8, 22, 36; Pl. 6, figs. i, j)

Type species.—*Mus marmota* Linnaeus.

Characters.—Phylogenetically significant differences between marmots and the other terrestrial sciurids are: cranium weakly inflated, skull greatly constricted postorbitally, dorsal surface greatly depressed anterior to superior nuchal line, subglobular in outline when viewed from above; rostrum nearly as large as cranium, more massive than in other sciurids except *Palaearctomys*; interorbital width much greater than postorbital width; anterior cranial fossa small; orbits small and temporal fossae large; ventral surface of basioccipital bone distinctively shaped (see page 275); P_4 as large as or larger than M_1 ; cheek teeth high crowned (see table 1); metaloph on M_1 and M_2 complete; metaloph on M_3 complete, turns posteriad to join posterior cingulum; P_4 molariform; protolophid of P_4 a transverse crest between bases of protoconid and parametaconid; occlusal outline of M_1 and M_2 parallelogram-shaped; pouch rudimentary, retractor muscles absent.

Cenotelic characters or characters of doubtful significance are: zygomatic

arches widely spread posteriorly, heavy at anterior ends; paroccipital processes large, extend below level of tympanic bullae; superior nuchal line prominent; angular process of mandible extends well beyond level of tip of condyloid process; coronoid process large; ventral mandibular incisure shallow; upper incisor stout, moderately curved, and longitudinally grooved; P^3 large (see table 1).

Remarks.—The marmot suprageneric group is an offshoot of the ground squirrel-prairie dog phyletic line which has become more fossorial in form than other squirrels. It is known by fossils from the Upper Miocene, at which time the group was differentiated from the other terrestrial squirrels. The genus *Marmota* is known by fossils from the Middle Pliocene which do not differ markedly from living species. It is now represented by a small number of species that are distributed throughout the Holarctic Region.

GROUND SQUIRREL-PRAIRIE DOG SUPRAGENERIC GROUP

Characters.—The ground squirrels and prairie dogs differ from the marmots in the following features: cranium moderately inflated; posterior part of dorsal surface of cranium slopes down to superior nuchal line, which is low or moderately raised; width of cranium greater in comparison with length; dorsal profile of skull convex; rostrum less massive, much smaller than cranium; width of skull at postorbital constriction equal to or greater than interorbital width; interorbital region of skull not massive; orbits larger than temporal fossae; basioccipital bone distinctively formed (see page 275); P^4 smaller than M^1 ; cheek pouches large or medium in size, retractor muscles present.

Characters which are cenotelic or of doubtful significance are: zygomatic arches appressed to skull or moderately widespread posteriorly; paroccipital processes short, not extending below level of tympanic bullae; parietal ridges low or moderately prominent; superior nuchal line low or moderately raised; enameled surfaces of incisors smooth.

Remarks.—The ground squirrel-prairie dog suprageneric group is limited in its distribution to the Nearctic Region, with the exception of some members of the subgenus *Citellus*. This distribution and the variety of forms present in the Nearctic Region strongly indicate that the group originated there.

Genus PROTOSPERMOPHILUS

(Pl. 7, figs. a, b, c)

Type species.—*Citellus (Protospermophilus) quatalensis* Gazin.

The characters and relationships of *Protospermophilus* are discussed on pages 348 and 355.

Genus AMMOSPERMOPHILUS

(Figs. 6, 20, 34; Pl. 3, figs. c, d)

Type species.—*Tamias leucurus* Merriam.

Characters.—Small masseteric tubercle situated directly below narrowly

oval infraorbital foramen, thus resembling *Otospermophilus* and *Callospermophilus*; outer wall of infraorbital foramen inclined slightly mediad. Anterior cranial fossa small and interorbital region of skull correspondingly narrow; postorbital constriction much wider than interorbital constriction. Cranium nearly rectangular in dorsal outline; dorsal surface flatter and less inclined downward to superior nuchal line than in other ground squirrels; sides and orbital surfaces nearly vertical. Cheek teeth low crowned; metaloph on M¹ and M² does not join protocone (see table 1); protolophid absent on P₄. Baculum distinctively shaped (see page 306). Clavobrachialis muscle absent; it is present in other terrestrial squirrels.

Characters of lesser or no phylogenetic importance are: ears short and round, color pattern distinctive (see page 260), posterior parts of zygomatic arches closely appressed to skull, process at anterior end of fossa on zygoma for origin of posterior part of masseter lateralis absent, coronoid process small as in *Xerospermophilus*, ventral mandibular incisure deep and acutely arched, upper incisor sharply curved, P³ small (see table 1), cheek pouches large. Tympanic bullae relatively larger and limbs relatively longer than those in other terrestrial sciurids.

Remarks.—Merriam (1892:27) first proposed *Ammospermophilus* as a subgenus of *Citellus* but gave no reasons for doing so. Mearns (1907:297) gave it generic rank and briefly characterized it. *Ammospermophilus* was considered a genus by most systematists from 1907 until 1938, when A. H. Howell reduced it to subgeneric rank.

Ammospermophilus is the most distinct group of ground squirrels and is definable on the basis of characters which have supraspecific phylogenetic significance. It differs from the other ground squirrels and resembles *Tamias* in several characters, most or all of which are cenotic, but which as a whole suggest that the group is not of recent origin. *Ammospermophilus* is not as well differentiated from the other ground squirrels as is the genus *Tamias*, but the relationship between *Ammospermophilus* and the other ground squirrels is not as close as that between the subgenera *Tamias* and *Neotamias* and is no closer than that between *Cynomys* and the other ground squirrels. It appears that *Ammospermophilus* has attained a degree of differentiation which is obscured by calling it a subgenus of *Citellus* and that its relationships are best shown by giving it generic rank.

Genus CITELLUS

Type species.—*Mus citellus* Linnaeus.

Remarks.—The genus *Citellus* is not a compact unit of closely related species as are *Tamias* and *Marmota*. The concept of the genus as applied here is more nearly comparable with the broader concept of the paleontologist than with the usually more restricted concept of the systematist working with living forms. The several kinds of ground squirrels reveal such a complex distribution and intermingling of characters that clearly definable groups, comparable in degree of differentiation to *Tamias* or *Marmota*, cannot be established.

The phyletic line of the ground squirrels and prairie dogs probably arose from *Protospermophilus*-like forms in the Upper Miocene and has since undergone rapid and diverse radiation. Segregation of the variable characters is not complete. The characters which distinguish the several groups of ground squirrels form a graded series or are distributed through the groups in a manner that prevents a clear separation of any one group on the basis of the phylogenetic criteria selected. If certain of the ground squirrels should become extinct, clearly definable genera would remain. Thus, if animals belonging only to the subgenera *Otospermophilus* and *Citellus* were known, these groups would assuredly be given generic rank. At the present stage in the evolutionary history of the ground squirrels the differentiation has not proceeded far enough or extinction has not occurred in the intermediate forms to a degree that permits generic recognition of any group except *Ammospermophilus*. In other words, some of the ground squirrels are in an evolutionary stage that falls in our system of classification between the subgenus and the genus. Furthermore, some of the groups have proceeded further in their differentiation than have others. The system of classification is devised for a static condition and cannot be satisfactorily applied to the particularly dynamic condition existing in the ground squirrels. The best, although still unsatisfactory, classification of ground squirrels is to place them (except *Ammospermophilus*) in one genus, to recognize the several groups as subgenera, and to indicate the relationships between the subgenera graphically.

Characters.—Masseteric tubercle of medium or large size, situated ventral and slightly lateral to infraorbital foramen; infraorbital foramen oval or subtriangular in shape, relatively broader than that in *Ammospermophilus*; cranium moderately inflated; dorsal outline of skull moderately convex; inflation of cranium in parietal region greater than that in *Ammospermophilus*, and posterior part of cranium slopes rapidly downward to superior nuchal line; a bend is present on dorsal surface of skull at junction of rostrum and cranium; process present at anterior end of fossa for origin of posterior part of masseter lateralis; zygomatic arches moderately or broadly expanded posteriorly, not appressed as closely as in *Ammospermophilus* and *Tamias* or spread as widely as in *Marmota*; squamosal roots of zygomatic arches directed laterad and ventrad; tympanic bullae moderately inflated; clavobrachialis muscle present; upper tooth rows parallel or converging only slightly posteriorly; M^3 and M_3 do not have complicated enamel folds in basins, thus resembling *Ammospermophilus* and differing from *Cynomys*.

Subgenus OTOSPERMOPHILUS

(Figs. 7, 21, 35, 45-47; Pl. 1, figs. *f*, *g*; Pl. 2, fig. *b*; Pl. 3, figs. *k*, *l*; Pl. 5, figs. *n*, *o*; Pl. 6, figs. *c'*, *f*, *g*, *h*)

Type species.—*Sciurus grammurus* Say.

Characters.—Infraorbital foramen oval, its lateral wall not inclined far laterad; masseteric tubercle situated nearly ventral to infraorbital foramen, not prominent as compared with the size of tubercle of subgenus *Citellus*; cranium broadly ovate; anterior cranial fossa large and interorbital region of skull cor-

respondingly broad; width at postorbital constriction slightly more than interorbital width; rostrum short and broad, not constricted at base; fossae anterolateral to incisive foramina deep; posterior mandibular incisure shallow; upper incisor stout and moderately curved; P_3 small; upper cheek teeth low crowned; M^1 and M^2 subquadrate in occlusal outline; trigon on P^4 - M^2 broadly V-shaped; metaloph on P^4 - M^2 separated from protocone by sulcus; mesostyles may or may not be present on P^4 - M^2 ; M^3 slightly larger than M^2 , posterior cingulum does not bend abruptly backward from protocone; metaloph on M^3 absent; protolophid on P_4 absent; P_4 not molariform (see page 287); protoconid of P_4 slightly larger than hypoconid; trigonid slightly higher than talonid on M_1 and M_2 ; occlusal outline of M_1 and M_2 rhomboidal. Baculum distinctively shaped (see page 306). Cheek pouches large.

Remarks.—*Otospermophilus* has retained more primitive characters than has any other subgenus in the genus *Citellus*, with the possible exception of *Callospermophilus*. This applies to the shape of the skull and the characters of the dentition and presumably is applicable to the form of the body, which is that of a generalized terrestrial type. The color pattern is unspecialized. *Citellus primitivus*, from the Upper Eocene, is an *Otospermophilus*-like form; and *Citellus gildleyi*, from the Middle Pliocene, is a member of this subgenus.

The subgenus *Notocitellus* was proposed by A. H. Howell (1938:44) for the Mexican ground squirrels, *C. annulatus* and *C. adocetus*. These species differ from *Otospermophilus* as defined by Howell as follows: ears shorter and less pointed, interorbital region relatively slightly broader, zygomatic arches slightly less expanded posteriorly, and incisors relatively heavier. The supraorbital foramina are always present in *Notocitellus* and may or may not be present in *Otospermophilus*. These differences do not appear to be of supra-specific significance, and the subgenus *Notocitellus* is considered a synonym of *Otospermophilus*.

Subgenus CALLOSPERMOPHILUS

(Figs. 3, 17, 31; Pl. 1, fig. b; Pl. 5, figs. b, c)

Type species.—*Sciurus lateralis* Say.

Characters.—Skull similar to that of *Otospermophilus*, differing from it as follows: smaller, interorbital region relatively narrower in comparison with width at postorbital constriction, angular process of mandible relatively shorter. Upper incisor slender, slightly curved, nearly perpendicular to basicranial axis; metaloph on M^1 and M^2 joins protocone; protolophid on P_4 small. Baculum resembles that of *Otospermophilus* but is smaller. Cheek pouches large; atlantoscapularis dorsalis muscle present. Color pattern distinctive (see page 260).

Remarks.—*Callospermophilus* and *Otospermophilus* are more closely related to each other than they are to other ground squirrels. They have been given generic rank by some systematists. If external features are not judged to be of generic significance, the differences between these two groups are not of generic magnitude. Consequently, if the differences between *Otospermophilus* and the ground squirrels other than *Callospermophilus* should be considered

sufficiently great to warrant giving *Otospermophilus* generic rank, *Callospermophilus* would become a subgenus of *Otospermophilus*.

Subgenus CITELLUS

(Figs. 2, 16, 30; Pl. 1, figs. c, e, h; Pl. 2, figs. h, i;
Pl. 3, figs. i, j; Pl. 5, figs. l, m)

Type species.—*Mus citellus* Linnaeus.

Characters.—Infraorbital foramen subtriangular in shape, its lateral wall inclined ventrolaterad; masseteric tubercle situated more laterally than that in *Otospermophilus* and usually relatively larger; cranium subglobular in dorsal outline, broad between squamosal roots of zygomatic arches, anterolateral walls markedly convergent; anterior cranial fossa small; interorbital and post-orbital constrictions narrow, approximately equal in width; zygomatic arches expanded posteriorly; rostrum short and broad, expanded at tip and constricted at base; fossae anterolateral to incisive foramina shallow; anterior margin of alveolar border drops abruptly to join diastema instead of merging with diastema in a gradual curve as in other subgenera; angular process of mandible longer than that in *Otospermophilus*. Upper incisor slender, slightly curved, and slightly procumbent; P³ large; cheek teeth high crowned; M¹ and M² narrowly triangular in occlusal outline; trigon on P⁴, M¹, and M² narrowly V-shaped; anterior cingulum joins protocone with abrupt change of direction on M¹ and M²; metaloph joins protocone on M¹ and M², and M³; mesostyles present or absent; M³ much larger than M²; posterior cingulum of M³ bends abruptly posteriad from protocone; P₄ molariform, protolophid large and extends obliquely ventromedial from protoconid, protoconid much larger than hypoconid; trigonid on lower cheek teeth much higher than talonid; occlusal outline of M₁ and M₂ parallelogram-shaped (for comparative outline of dental characters, see table 1). Baculum distinctively shaped (see page 306). Cheek pouches of medium size; atlantoscapularis dorsalis muscle absent.

Remarks.—The members of the subgenus *Citellus* are the most highly specialized ground squirrels in regard to the external features and dentition and are at the opposite extreme of the genus from *Otospermophilus*. The subgenus *Citellus* resembles *Cynomys* more closely than it resembles the other subgenera of ground squirrels in most of the features of the skull and dentition. The reasons for referring the prairie dogs to a separate genus are given on pages 374 and 381.

The great variety of ground squirrels in North America and their present distribution indicate that the center of their origin was in the western part of the United States. The members of the subgenus *Citellus* occur in the north-western part of the United States, western Canada, Alaska, and Eurasia. All of the Eurasian ground squirrels are members of this subgenus. Fossil forms belonging to the subgenus *Citellus* are not known from deposits older than the Pleistocene of North America, Europe, and Asia. These facts suggest that the subgenus *Citellus* originated in North America during the Pliocene and that some of its members migrated to Asia and Europe during the Pleistocene.

Subgenus ICTIDOMYS

(Figs. 4, 78, 32; Pl. 3, figs. g, h; Pl. 5, figs. h-k)

Type species.—*Sciurus tridecemlineatus* Mitchell.

Characters.—Skull more variable in shape than that in other subgenus of *Citellus*; outline of cranium nearly quadrate as in *Xerospermophilus*, width may be greater than length or *vice versa*; anterolateral walls of cranium nearly vertical, not inclined anteriorly as much as in *Otospermophilus*, *Poliocitellus*, and subgenus *Citellus*; anterior cranial fossa small; width at postorbital constriction relatively broader than in subgenus *Citellus* and relatively narrower than in *Xerospermophilus*, slightly greater than width of interorbital region; masseteric tubercle and infraorbital foramen usually as in subgenus *Citellus*; rostrum short or moderately long, not constricted at base; fossae anterolateral to incisive foramen usually moderately deep; ventral mandibular incisure deep and acutely arched as in *Xerospermophilus*. Upper incisor stouter than that of *Callospermophilus* and smaller than that of *Otospermophilus*, markedly curved; P³ of medium size; crowns of cheek teeth higher than those of *Otospermophilus* and lower than those of subgenus *Citellus*; trigon on P⁴, M¹, and M² narrowly V-shaped; anterior cingulum on M¹ and M² joins protocone with abrupt change of direction; metaloph on M¹ and M² separated from protocone by sulcus; tendency toward fusion of metaconule and metacone on M¹ and M². Metaloph indistinct or absent on M³; M³ much larger than M²; mesostyles present or absent; posterior cingulum on M³ bends abruptly posteriad from protocone; P₄ not molariform, protolophid small; trigonid of lower cheek teeth much higher than talonid, slightly lower than trigonid of cheek teeth of subgenus *Citellus*; occlusal outline of M₁ and M₂ rhomboidal (for comparative outline of features of dentition see table 1). Baculum variable in shape (see page 306). Cheek pouches of medium size; atlantoscapularis dorsalis muscle absent.

Remarks.—On the basis of the dentition, *Ictidomys* is more closely related to the subgenus *Citellus* than to other ground squirrels. The forms of the cranium, rostrum, and baculum are specifically variable. It appears that the species assigned to this subgenus, *C. mexicanus*, *C. tridecemlineatus*, *C. spilosoma*, and *C. perotensis*, are not as closely related as are the species in each of the other subgenera of *Citellus*. The baculum and color pattern of *C. spilosoma* and presumably of *C. perotensis* (baculum not examined) are markedly different from the corresponding features of *C. mexicanus* and *C. tridecemlineatus*.

Subgenus XEROSPERMOPHILUS

(Figs. 1, 15, 29; Pl. 1, fig. a; Pl. 3, figs. e, f; Pl. 5, figs. d-g)

Type species.—*Spermophilus mohavensis* Merriam.

Characters.—Skull short and broad, similar in general appearance to skull of smaller species of subgenus *Citellus*; cranium short and broad, anterolateral walls less convergent than in subgenus *Citellus*; width of postorbital constriction relatively about as in *Otospermophilus*, much greater than width of narrow interorbital region; rostrum short as in *Ammospermophilus*, not constrict-

ed at base or expanded at tip; coronoid process of mandible smaller than that in other subgenera of *Citellus*; ventral mandibular incisure deep and acutely arched as in *Ictidomys*; other parts of skull as in subgenus *Citellus*. Upper incisor usually more curved; P^3 smaller than in other subgenera of *Citellus*, slightly larger than in *Ammospermophilus*; molar teeth low crowned; M^1 and M^2 subquadrate in occlusal outline; trigon on P^4 , M^1 and M^2 broadly V-shaped; anterior cingulum usually joins protocone with abrupt change of direction on M^1 and M^2 ; metaloph on P^4 , M^1 and M^2 separated from protocone by sulcus as in *Otospermophilus* and *Ictidomys*; mesostyles absent; M^3 slightly larger than M^2 ; posterior cingulum of M^3 does not bend sharply posteriad from protocone as it does in subgenus *Citellus* and *Ictidomys*; P_4 not molariform; protolophid small; trigonid on lower cheek teeth slightly higher than talonid; occlusal outline of M_1 and M_2 rhomboidal as in *Otospermophilus* (for comparative outline of dental characters see table 1). Baculum similar to that in subgenus *Citellus* (see page 306). Cheek pouches small; atlantoscapularis dorsalis muscle absent.

Remarks.—In external appearance and form of baculum, *Xerospermophilus* resembles the subgenus *Citellus*. The cranium is similar to that in *Ictidomys*. The teeth most closely resemble those of *Otospermophilus* or *Ammospermophilus*.

Subgenus POLIOCITELLUS

(Figs. 5, 19, 33; Pl. 1, d; Pl. 3, figs. m, n; Pl. 5, fig. a)

Type species.—*Arctomys franklinii* Sabine.

Characters.—Skull long and narrow; outline of cranium ovate as in *Otospermophilus*, but cranium relatively longer and narrower; postorbital width about equal to interorbital width, both widths narrow as in subgenera *Citellus* and *Ictidomys*; rostrum relatively longer and slenderer than in other Nearctic sciurids, not constricted at base; fossae anterolateral to incisive foramina moderately deep; infraorbital foramen and masseteric tubercle as in subgenus *Citellus*; anterior cranial fossa relatively larger than that in *Ictidomys*, *Xerospermophilus*, and subgenus *Citellus* and smaller than in *Otospermophilus*; mandible as in *Otospermophilus*. Upper incisor as in *Callospermophilus*, stouter than that of subgenus *Citellus* and smaller than that in *Otospermophilus*; P^3 moderately large; molars moderately high-crowned, higher than in *Otospermophilus* and lower than in subgenus *Citellus*; M^1 and M^2 subquadrate in occlusal outline; trigon on P^4 , M^1 and M^2 broadly V-shaped; anterior cingulum usually joins protocone with abrupt change of direction; metalophs complete and mesostyles present on P^4 , M^1 and M^2 ; M^3 slightly larger than M^2 ; posterior cingulum on M^3 as in *Otospermophilus*; P_4 nearly molariform, protolophid a transverse ridge between bases of protoconid and parametaconid; trigonid on lower cheek teeth somewhat higher than talonid; occlusal outline of M_1 and M_2 rhomboidal (for comparative outline of dental characters, see table 1). Baculum resembles that of subgenus *Citellus* (see page 306). Cheek pouches large; atlantoscapularis dorsalis muscle absent.

Remarks.—The skull resembles that of *Otospermophilus* more closely than

it resembles the skull of other subgenera, but it also has marked resemblances to the skull of *Ictidomys*. *Poliocitellus* is a clearly characterized subgenus that appears to be most closely related to *Callospermophilus* and *Otospermophilus*. In several features of the dentition it is intermediate between these subgenera and the subgenera *Ictidomys* and *Citellus*.

Genus CYNOMYS

(Figs. 9, 23, 37; Pl. 2, fig. c; Pl. 4)

Type species.—*Cynomys socialis* Rafinesque.

Characters.—Skull and dentition similar to those of subgenus *Citellus*, differing as follows: masseteric tubercle larger; squamosal roots of zygomatica extend slightly posteriad from skull; P^3 larger; maxillary tooth rows markedly convergent posteriorly; protomeres of upper cheek teeth (except P^3) higher and inclined more nearly laterad; M^3 larger in comparison with size of M^2 ; complex enamel folds present in basin of M^3 , an enamel ridge extends medially from lateral margin between protoloph and metaloph; protolophid on P_4 joins protoconid and parametaconid; complicated enamel folds present in talonid basin of M_3 and usually in basins of M_1 and M_2 (for comparative outline of dental characters, see table 1). Baculum distinctively shaped (see page 306); most closely resembles baculum of *Xerospermophilus*. Cheek pouch small; atlantoscaphularis dorsalis muscle present.

Remarks.—In the features of the skull and most of the dental characters *Cynomys* resembles the subgenus *Citellus* even more closely than do the other subgenera of ground squirrels (genus *Citellus*), with the possible exception of *Ictidomys*. *Cynomys* and the subgenus *Citellus* are closely related or convergence has occurred to a marked degree. The first alternative appears more probable. *Cynomys* is given generic rank because of the highly specialized and distinctive dentition.

Tree Squirrel Division

Characters.—The characters which are morphologically comparable to those that were judged to have phylogenetic significance in the terrestrial squirrel and chipmunk division, are: infraorbital foramen an anteroventrally inclined slit situated well anterior to P^3 ; masseteric tubercle small, situated anteroventral to infraorbital foramen; fossa on anterior surface of zygomatic plate for origin of masseter lateralis broad, long, and slightly convex; maxillonasalis muscle does not arise on dorsolateral margin of zygomatic plate and this margin not crested; anterodorsal margin of fossa terminates anterior to premaxillary-maxillary suture; zygomatic plate tilted upward at an angle of about 60° to basicranial axis, intermediate in inclination between flying squirrels and terrestrial squirrels; zygomatica appressed and nearly parallel, sides nearly vertical; fossa on lateral surface of zygoma for origin of posterior part of masseter lateralis restricted to lower part of arch; premaxillary-maxillary suture crosses anterior part of zygomatic plate, runs ventrad toward infraorbital foramen, and curves anteroventrad to incisive foramen; anterior cranial fossa large; interorbital region of skull broader than in other sciurids; cranium more inflated than in terrestrial squirrels, broad postorbitally; diastemal part

of mandible short and deep; anterior tip of mandible situated below level of alveolar border; coronoid process small; base of condyloid process wider than in other sciurids, dorsal margin of process well above level of mandibular tooth row; angular process quadrate or rounded, not drawn out into a process at posterodorsal angle; incisor teeth markedly flattened, narrow and deep; on M^1 and M^2 protocone nearly as wide as labial margin, occlusal outline quadrate, lophs nearly parallel; on M^1 and M^2 hypoconid larger than protoconid, entoconid distinct, entoconid region angular, posterolophid straight; cheek pouches absent. Other characters comparable to those of terrestrial squirrel and chipmunk group are: frontal processes present on jugal bones; eight true ribs present; manubrium triangular, pointed anteriorly; metacromion, acromion, and coracoid process distinctively shaped (see page 296); second sacral vertebra not included in pelvic articulation; maxillonasalis muscle arises by one head; platysma 4 not attached to metacromion.

Paleotelic characters comparable to those of the terrestrial squirrel and chipmunk sections are: infraorbital canal present; notches in ventral surfaces of zygomatic plates opposite M^1 or posterior part of P^4 ; ectolophids low and nearly marginal; mesoconids present on M^1 and M^2 ; baculum of distinctive type (see page 306) or absent. Other characters equivalent to those distinguishing between the chipmunk and terrestrial squirrel sections are: ears and claws of distinctive types (see pages 261-262); digits in order of increasing length 1-5-2-3-4; rostrum relatively deep and narrow; supraorbital notches situated near plane of zygomatic notches; pterygoid fossae narrow, interpterygoid fossa broad, and lateral pterygoid plates rudimentary; P^4 not molariform (see page 287); teres major fossa of scapula a long, deep groove; one subscapular ridge present; os coxae of distinctive type (see page 301).

Other characters of tree squirrels are: postorbital constriction of skull relatively wider than in other sciurids, about equal to interorbital width; enamel surfaces of incisors finely crenulated; P^3 minute or absent; molars low-crowned; M^3 slightly or no larger than M^2 ; metalophs complete and mesostyles present on M^1 and M^2 ; metaloph on M^3 obsolete; trigonid about equal in height to talonid on lower cheek teeth; three sacral vertebrae present.

Genus SCIURUS

(Figs. 14, 28, 42, 44; Pl. 2, fig. a; Pl. 6, figs. c, d; Pl. 8, figs. c, e)

Type species.—*Sciurus vulgaris* Linnaeus.

Characters.—The notches in the ventral surface of the zygomatic plates are opposite M^1 , and the baculum is distinctively shaped (see page 306). In comparison with *Tamiasciurus* the dorsal outline of the skull is more convex, the cranium is more inflated, the rostrum is relatively longer, the zygomata are less closely appressed, the angular process of the mandible is rounded, and the ventral mandibular incisure is less concave.

Genus TAMIASCIURUS

(Figs. 12, 26, 40; Pl. 6, figs. a, b)

Type species.—*Sciurus hudsonicus* Erxleben.

Characters.—The notch in the zygomatic plate is opposite the anterior margin of M^1 or the posterior part of P^4 and is farther forward than in *Sciurus*. Other differences from *Sciurus* are stated in the preceding paragraph. The male reproductive system is markedly different from that of *Sciurus* (Mossman, Lawlah, and Bradley, 1932:119-126), and the baculum is absent.

As determined by a study of the osteological and myological features, *Tamiasciurus* bears approximately the same relation to *Sciurus* as the subgenus *Tamias* does to *Neotamias*, and is not generically distinct from *Sciurus*. The differences in the reproductive system are here considered to be of generic significance. However, insufficient work has been done on the reproductive systems of squirrels to provide a basis for an adequate interpretation of the value of this system in determining phylogenetic relationships within the group.

Flying Squirrel Division

Genus GLAUCOMYS

(Figs. 13, 27, 41; Pl. 3, figs. a, b)

Type species.—*Mus volans* Linnaeus.

Characters.—The characters morphologically comparable to the phylogenetically significant characters of the terrestrial squirrel and chipmunk division are: infraorbital foramen oval, vertical, and situated near P^3 ; masseteric tubercle small and located directly below the foramen as in *Ammospermophilus*; fossa on anterior surface of zygomatic plate broad, short, and slightly convex; maxillonasalis muscle does not arise on dorsolateral margin of fossa and margin not crested; anterodorsal margin of fossa rounded and terminates at premaxillary-maxillary suture; zygomatic plate tilted upward at an angle of approximately 65° to basicranial axis, more nearly vertical than that in other Nearctic sciurids; in correlation with uptilting of zygomatic plate, the dorsal edge of plate is situated farther posteriorly and the infraorbital foramen appears to be situated farther anteriorly than in terrestrial squirrels and chipmunks; zygomata appressed and slightly convergent anteriorly, sides nearly vertical (not twisted as in terrestrial squirrels and chipmunks); fossa on lateral surface of zygoma restricted to lower part of arch; premaxillary-maxillary suture as in terrestrial squirrels and chipmunks; interorbital region of skull narrow; cranium more inflated than in tree squirrels; diastemal part of mandible relatively short and deep; anterior tip of mandible situated below level of alveolar border; coronoid process small; base of condyloid process wide, dorsal margin of process well above level of mandibular tooth row; angular process quadrate; incisors not markedly flattened; on M^1 and M^2 protocone approximately as wide as labial margin, occlusal outline quadrate, lophs nearly parallel; on M_1 and M_2 hypoconid not larger than protoconid, entoconid distinct, entoconid region angular, posterolophid crescentic; cheek pouches absent. Other characters comparable to those of chipmunk and terrestrial squirrel group are: no frontal process on jugal bone; seven true ribs present; manubrium Y-shaped; metacromion, acromion, and coracoid process of scapula distinctively shaped (see page 296) second sacral vertebra not included in pelvic articulation; maxillonasalis muscle arises by one head; platysma 4 does not attach to metacromion.

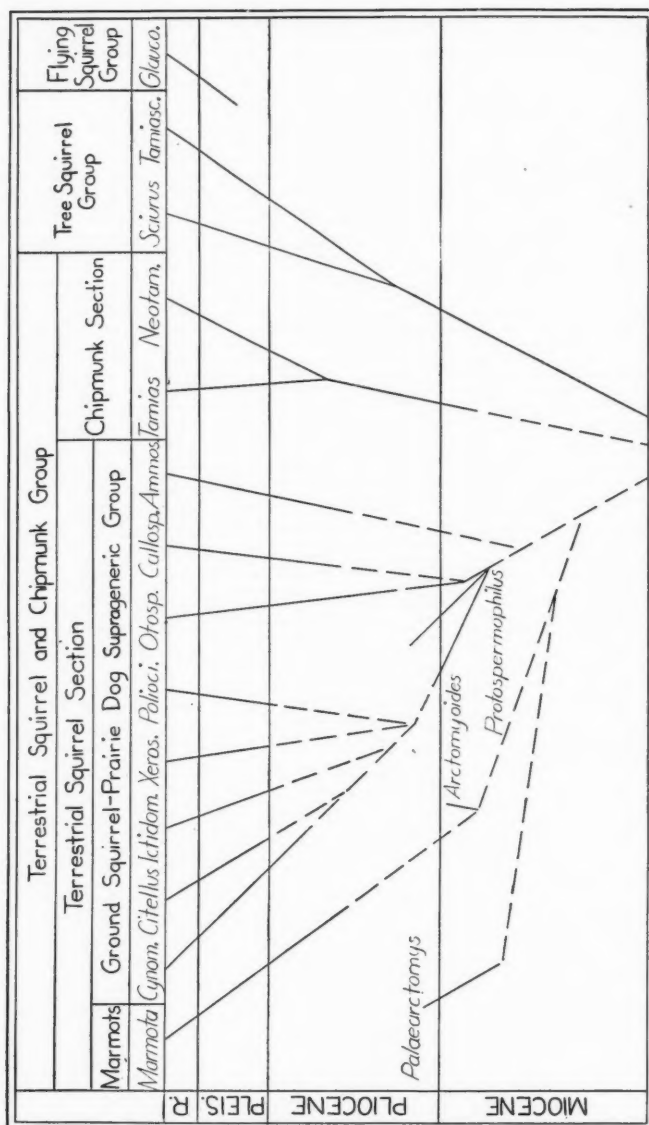


Fig. 48. Chart showing phylogenetic relationships of Nearctic Sciuridae.

Paleotelic characters comparable to those of the terrestrial squirrel and chipmunk sections are: infraorbital canal present; notches in ventral surfaces of zygomatic plates opposite P^4 ; width of plates between zygomatic notches and infraorbital foramina correspondingly narrow; ectolophids low and submarginal; mesoconids present on M_1 and M_2 ; baculum of distinctive type (see page 306). Other characters equivalent to those which differentiate between the chipmunk and terrestrial squirrel sections are: gliding membrane present, ears and claws of distinctive types (see pages 261-262); digits in order of increasing length 1-(2.5)-(3.4); supraorbital notches situated posterior to plane of zygomatic notches; pterygoid fossae narrow, interpterygoid fossa broad, and lateral pterygoid plates rudimentary; P^4 not molariform (see page 287); teres major fossa of scapula a definite groove, long and shallow; one subscapular ridge present; os coxae of distinctive form (see page 301).

Other characters of *Glaucomys* are: postorbital constriction of skull narrow, approximately equal to width of interorbital constriction; mastoid bone inflated; upper incisor slender, procumbent, and slightly curved; enamel surfaces of incisors usually finely crenulated; P^3 small (see table 1 for details of dental characters); molar teeth low crowned; M^3 slightly or no larger than M^2 ; on M^1 and M^2 metaloph joins protocone, mesostyles absent; metaloph on M^3 obsolete; trigonid slightly higher than talonid on lower cheek teeth; narrow groove present in margin of M_1 and M_2 anterior to protoconid; three sacral vertebrae present; length of pubic symphysis less than width; sternoauricularis muscle absent; platysma and cutaneous maximus muscles highly specialized in correlation with presence of gliding membrane.

Remarks.—*Glaucomys* has many features in common with tree squirrels as opposed to terrestrial squirrels and chipmunks, and *vice versa*. The zygomatic arches and plates resemble those of tree squirrels, and the infraorbital area and premaxillary-maxillary suture are like those in terrestrial squirrels. The dentition does not clarify the relationships between *Glaucomys* and the other two groups of Nearctic squirrels. The mandible more closely resembles that of tree squirrels.

The following characters distinguish the tree squirrels, terrestrial squirrels, and chipmunks from *Glaucomys*: gliding membrane absent, vibrissal arrangement distinctive (see page 260), and sternoauricular muscle present. These characters do not appear to have broad phylogenetic significance.

The information obtained in this study does not permit one to determine whether the flying squirrel is more closely related to the tree squirrel or to the terrestrial squirrel and chipmunk group. Consequently, the separation of the squirrels into the subfamilies Pteromyinae and Sciurinae appears to be untenable. A division of the family Sciuridae into three subfamilies would accord with the data concerning Nearctic squirrels, but the scope of the present study is geographically limited and does not justify such a division of the squirrels of the world.

The fact that there are no North American fossils of *Glaucomys* known from deposits older than the Pleistocene and that closely related forms are known from the Pliocene of Europe and Asia indicates that the flying squirrels

are a recent addition to the fauna of North America. The present distribution of flying squirrels provides supporting evidence.

Conclusion

The phylogenetic relationships of the Nearctic Sciuridae, as determined by a comparative study of the external features, osteology, myology and paleontology, are shown in the phylogenetic tree (see page 384) and the following outline of classification.

Outline of Classification

Family Sciuridae

Terrestrial Squirrel and Chipmunk Division

Chipmunk Section

Genus *Tamias*

Subgenus *Tamias*

Subgenus *Neotamias*

Terrestrial Squirrel Section

Marmot Suprageneric Group

Genus *Palaeocitellus*

Genus *Arctomys*

Genus *Marmota*

Ground Squirrel and Prairie Dog Suprageneric Group

Genus *Perognathomys*

Genus *Ammodontomys*

Genus *Citellus*

Subgenus *Otospermophilus*

Subgenus *Callospermophilus*

Subgenus *Citellus*

Subgenus *Ictodromus*

Subgenus *Xerospermophilus*

Subgenus *Poliocitellus*

Genus *Cynomys*

Tree Squirrel Division

Genus *Sciurus*

Genus *Tamiasciurus*

Flying Squirrel Division

Genus *Glaucomys*

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Records and Descriptions of North American Crane-Flies (Diptera)¹

Part V. Tipuloidea of the Grand Teton National Park and Teton National Forest, Wyoming

Charles P. Alexander

In continuation of the series of papers considering the rich crane-fly fauna of the western North American states and provinces, the present report concerns one of the most beautiful and striking sections of the entire United States, the Grand Teton National Park and vicinity. As was done in previous instalments, illustrations of new and little-known species are provided since it is certain that such aid materially in the correct determination of the various forms. The recent publication of the "Crane-flies of Connecticut"² has made available keys and figures for the species now known from north-eastern North America. With this as a basis it is intended in the present paper and succeeding reports under this title to figure such species that have not been so illustrated.

General Account

The Grand Teton National Park, embracing the more striking peaks of the Teton Range, northwestern Wyoming, has an area of approximately 150 square miles or 96,000 acres. The park has a length of 27 miles, with a width varying from 3 to 9 miles. Its northern extremity lies approximately 11 miles south of the southern boundary of the Yellowstone National Park (see Part IV of this series of papers; Alexander 1943). Despite the close proximity of the two parks, a marked difference in the crane-flies was found that cannot be attributed to seasonal collecting, since the major series of flies available for study from both areas was taken at approximately the same time of year, representing the late spring and early summer fauna. The apparent reason for the differences lies in certain very distinct ecological conditions existing in the two areas (compare Stations 1 and 2 of present paper). As indicated by the present title, I am including not only the species of crane-flies known from the National Park but also from certain selected stations

¹ The preceding part under this general title was published in the American Midland Naturalist 30:718-764; 1943.

References in the text refer to the bibliography at the conclusion of the general account.

In all cases in this report where no collector is given, the specimens were secured by the author. M. M. Alexander—Mrs. Charles P. Alexander.

² Alexander, Charles P. The Diptera or true flies of Connecticut. Tanyderidae, Ptychopteridae, Trichoceridae, Anisopodidae, Tipulidae. Conn. State Geol. and Nat. Hist. Surv. Bull. 64:183-486, index 501-509; figs. 18-55 (with 389 individual illustrations); 1942 (published in 1943).

in the adjoining Teton National Forest, a vast area bordering the Park on the east and extending northward to the limits of the Yellowstone National Park and the Shoshone National Forest. Very recently a further noteworthy addition to the national holdings in the Grand Teton section was made by the setting aside of the Jackson Hole National Monument, established by order of President Franklin D. Roosevelt in the spring of 1943, including nearly 220,000 acres of land to the south and southeast of the Park in the Jackson Hole country.

As was indicated in the preceding part, the first white man to see the Tetons was John Colter, who, in the winter of 1807-1808, passed through the Jackson Hole at the foot of the Teton Range. In the autumn of 1811, the Astorians, under the leadership of Mr. Wilson Price Hunt, crossed the range through the Teton Pass. Washington Irving, in "Astoria", has described this in detail. Two short paragraphs may be quoted from this classic. September 15, 1811. "In the course of the day they came to a height that commanded an almost boundless prospect. Here one of the guides paused, and, after considering the vast landscape attentively, pointed to three mountain peaks glistening with snow, which rose, he said, above a fork of the Columbia River. * * * These remarkable peaks are known to some travelers as the Tetons." And still later in September. "An important point in their arduous journey had been attained, a few miles from their camp rose the three vast snowy peaks called the Tetons."

Atwood (1940) speaks of the Grand Teton National Park as being "one of the scenic wonderlands of the world." To anyone visiting the area in mid-June, when the mountains are still chiefly snowclad, the above characterization does not seem exaggerated. In its essentials, the National Park consists of the Teton Range, with its series of giant peaks separated by deep canyons, at the foot of each of the latter with a beautiful lake. From north to south, these lakes draining into Cottonwood Creek and thence into the Snake River, include Leigh (altitude 6,870 feet); String or Beaver Dick (6,867 feet); Jenny (6,779 feet) and Bradley (7,061 feet). Still farther to the south at the foot of Death Canyon and draining directly into the Snake is one of the most beautiful of all the lakes, Phelps (6,615 feet). The mountains that concern us chiefly are, from north to south, Mount Moran (12,100 feet), separated from the St. John Range by Indian Paintbrush Canyon and Leigh Canyon; the various peaks of the St. John Range between Leigh Creek on the north and Cascade Creek on the south; the great mass of the Teton Range proper, with the various giants, Owen, Grand Teton (13,766 feet), Teewinot, Middle Teton, South Teton and Nez-Perce, with others. Still farther to the south the peaks become lower but are still impressive and very beautiful. The southern end of the range is marked by the Teton Pass (8,429 feet), permitting travel into Idaho.

From the eastern or Jackson Hole side, the Teton Range presents an unusually precipitous front, rising abruptly from the floor of the valley (about 6,500 feet) to the maximum height of more than 13,760 feet. Glaciers of the Ice Age have played the chief role in sculpturing the valleys and altering the floor of the Hole. Each of the various main canyons contained its own local

glacier, all emptying onto the floor of Jackson Hole. The signs of the last stages of the glacier are to be seen everywhere in the moraines, outwash plains, lakes and canyons.

The various canyons permit easiest access into the heart of the range. Those most used by our party in 1941 and 1942 were Indian Paintbrush Canyon, Cascade Canyon and Death Canyon, the latter the most southerly. Cascade Canyon, between the St. John peaks and the three Teton giants was especially favorable and accessible. Cascade Creek, often a roaring mountain torrent from melting snow, flows down the canyon and may be followed for several miles along a well-maintained park trail. Near the head of the north fork of Cascade Creek, one reaches a beautiful mountain tarn, Lake Solitude (9,024 feet), close to the extreme western boundary of the park. Shortly before it flows into Jenny Lake, Cascade Creek forms one of the most beautiful falls in the region, Hidden Falls, where numerous crane-flies were taken, as discussed later. The Indian Paintbrush and Death Canyon trails were similarly followed for several miles and excellent collecting found, particularly at middle altitudes.

Life Zones.—Of the seven life zones or faunal areas recognized by Merriam and his successors, four are to be found within the geographical limits considered in this report.

Transition (Foothills). The valley of the upper Snake River in the Jackson Hole country, between the towns of Moran and Jackson. This includes the floor of the "Hole" to an altitude of about 6,700 feet. This is noteworthy as being one of the chief winter reserves of the American elk in this region. Station No. 1 (Arizona Creek) is definitely in this zone; Station No. 2 (Moran bog), while lying within the limits of the Transition shows definite features of the next zone.

Canadian (Montane). Much of the country surrounding the foot of the Teton Range, including the various lakes as discussed before; thence up the lower mountain slopes and canyons to the upper limits of large tree growth, or approximately 8,000—9,000 feet, dependent on exposure. Lake Solitude (9,024 feet) and Twogwotee Pass (9,650 feet) show some features of the highest Canadian, yet appear to fall in the succeeding zone. Virtually all collections of crane-flies made by the author and colleagues in 1941 and 1942 are from the Canadian zone.

Hudsonian (Subalpine). The relatively narrow belt of scrubby tree growth above the Canadian zone and below the limits of extreme timberline. As mentioned, Lake Solitude and Twogwotee Pass seem to pertain to this zone.

Arctic-Alpine (Alpine). The high mountain country above extreme timber line on the highest peaks and ridges. Because of the unusual number of major mountain peaks in the Teton Range, a considerable proportion of the park lies within this zone.

(References to life zones of the Tetons: Bailey, 1930: 9-15, colored map showing the life zones; Cary, 1917, colored map; best sources for this region.)

The more recent classification of North America into biotic provinces (Dice, 1943) places all of northwestern Wyoming in the Montanian Province, which here attains its southern limits, thence extending far to the northwest to include the western third of Montana, northern half of Idaho, much of the southern half of British Columbia, together with the adjoining portions of Alberta, and a comparatively narrow arm extending westward in northern Washington. The distribution of Tipulidae confirms that this arrangement of states and provinces is a natural one.

The Fenneman (1931) classification of the United States into physical divisions places the Grand Teton region in the Middle Rocky Mountain Province of the Rocky Mountain System. Mulford's division of the country on the basis of plant-growth regions (Van Dersal, 1938: 16-27, map) places all of northwestern Wyoming in the Northern Rocky Mountain Region.

All streams within the Park limits eventually drain into the Snake River, a chief tributary of the Columbia. All collections were made to the west of the Continental Divide.

Collecting Stations.—Although collections of crane-flies were made in many scattered places within the area under consideration, a few localities proved to be of such importance that they were made the basis of special investigation.

The chief collections available for this study were those made in 1941 by the author and Mrs. Alexander, with the appreciated co-operation of Mr. and Mrs. Walter H. Harrison, of Amherst, Massachusetts, our companions on many trips to various sections of the United States and Canada. These collections were made between the dates of July 1st and 15th, representing the late spring and early summer fauna. In 1942, Mrs. Alexander and I again camped in the Park and collected between the dates of July 1st and 10th. As indicated in an earlier paper, this second trip was a great disappointment in that I suffered a serious foot injury on July 1st, this necessitating hospital treatment in Jackson and restricting possible collecting trips to a very few where transportation by car was possible and but little walking or hobbling was required in order to secure at least a few specimens (Station 1, Arizona Creek; Station 3, Hidden Falls; Station 6, Twogwotee Pass: this last proved to be of exceptional interest and added several species of these flies to those previously known from the area). Besides the above lots of material, totalling some thousands of specimens, only one further major series from the Teton Area has been available to me. This included several specimens taken by Mr. and Mrs. John L. Sperry, of Riverside, California, taken chiefly along Pilgrim Creek, near Moran, and in the Indian Paintbrush Canyon, in the Park proper. Many of these latter specimens were captured at a date later than any indicated above and represent the late summer or early autumn fauna. Among these late season species, especially, were found various additions to the present list.

The base stations established by us in 1941 and 1942 are as follows:

1. Arizona Creek; altitude 6,790 feet, July 1, 2, 8, and 15, 1941; July 4, 1942. Arizona Creek rises on Wildcat Peak in the Teton National Forest, and

flows southwest into Jackson Lake. At the point where Route 89 (287) crosses the creek unusually rich collecting was found. The country is definitely in the Transition lifezone, which probably accounts for the fact that many of the species of Tipulidae found here were different from those of the Canadian or Hudsonian zones in either the Yellowstone or Grand Teton National Parks. The sparse woody cover along the creek and nearby consists especially of Engelmann spruce, *Picea engelmannii* (Parry) Engelm., and alpine fir, *Abies lasiocarpa* (Hook.) Nutt., with mountain alder, *Alnus tenuifolia* Nutt., species of willow, *Salix* sp., and bog birch, *Betula glandulosa* Michx.; further growths of *Shepherdia*, *Cornus stolonifera* Michx., and *Lonicera involucrata* (Richards) Banks. Most of the Tipulidae were swept from the rank herbage consisting primarily of *Equisetum arvense* L., *E. hiemale* L., *Smilacina stellata* (L.) Desf., *Actaea arguta* Nutt., *Heracleum lanatum* Michx., *Pedicularis groenlandica* Retz., *Castilleja* sp. (red flowered), and *Rudbeckia occidentalis* Nutt. Some of the more characteristic Tipulidae of this station include *Dicranoptycha quadrivittata* Alexander, *Dicranota* (*Dicranota*) *montana* Alexander, *Limnophila* (*Elaeophila*) *aleator* sp. nov., *Hexatoma* (*Eriocera*) *velveta* (Doane), *Gonomyia* (*Gonomyia*) *aciculifera* Alexander, *Rhabdomastix* (*Sacandaga*) *neolurida* Alexander, *Erioptera* (*Psiloonopa*) *gaspicola* (Alexander), *E. (P.) shoshone* sp. nov., *E. (Ilisia) bispinigera* Alexander, *E. (I.) manitobensis* Alexander, *E. (I.) zukeli* Alexander, *Ormosia megarhabda* Alexander, *O. tetonica* sp. nov., *Molophilus* (*Molophilus*) *harrisoni* sp. nov.; *M. (M.) perflaveolus* Alexander. The above list provides an idea of the extreme richness of this particular station. Labelled "Arizona Creek."

2. Moran. Teton National Forest; a large bog, 2.4 miles north of the village of Moran; altitude 6,800 feet, July 2 and 5, 1941. Around the bog margin numerous lodgepole pine, *Pinus murrayana* Balf., with fewer alpine fir and much aspen, *Populus tremuloides* Michx. On the hummocks of the bog proper, extensive thickets of willow, the dominant shrub. The herbage included extensive beds of *Equisetum arvense* between the willow thickets; *Limnorchis borealis* (Cham.) Rydb., *L. viridiflora* (Cham.) Rydb., *Camassia esculenta* Lindl., *Geranium Richardsonii* F. & M., *Mimulus Langsdorfii* Sims., and *Pedicularis groenlandica*, the latter in the very wet places. Some of the more interesting crane-flies included *Tipula sulphurea jacksonensis* subsp. nov.; *Dicranota* (*Polyangaeus*) *megalops* sp. nov.; *Limnophila* (*Phylidorea*) *platyphallus* Alexander. Labelled "Moran."

3. Hidden Falls, Cascade Creek, Grand Teton National Park; altitude 6,900-7,000 feet, July 3, 4, 1941; July 8, 1942. Collections under this heading include especially those made on shaded earthen banks along the trail below the falls. These banks were shaded by alpine fir, Greene Mountain Ash, *Sorbus scopulina* Greene; *Rubus parviflorus* Nutt.; *Acer glabrum* Torrey; species of *Ribes*, as *R. lacustre* (Pers.) Poir., and *R. parvulum* (Gray) Rydb., and other low shrubs. On the moist banks beneath this shade occurred a rank growth of liverworts, including *Marchantia*, and various mosses. In this habitat occurred *Ornithodes harrimani* Coq., *Dicranota* (*Polyangaeus*) *subapterogyne* Alex., *Archilimnophila subunica* (Alexander) and others. Also

near the falls occurred various low cliffs and rock outcroppings, on the dripping faces and slopes of which occurred a sparse but characteristic lithophytic association. Some of the characteristic Tipulidae of this habitat included *Limonia (Dicranomyia) citrina* (Doane), *Elliptera astigmatica* Alexander, and *Phyllolabis lagganensis* Alexander. Labelled "Hidden Falls."

4. Cascade Canyon trail to Lake Solitude; boggy area at 8,200 feet, July 9, 1941. An extensive oxylophytic area on the mountain side, with several streams and cold springs. The tree growth included scattered low trees of alpine fir and whitebark pine, *Pinus albicaulis* Engelm. Shrubs scattered about included *Salix* sp., dominant; *Betula glandulosa*; *Spiraea densiflora* Nutt., and three very characteristic heaths, *Kalmia polifolia* Wang, *Phyllodoce empetriformis* (Smith) Don., and *Menziesia ferruginea* Smith. In the streamlets of the boggy areas, various herbs as *Limnorchis borealis*, *L. viridiflora*, *Camassia esculenta*, *Mitella pentandra* Hook., and *Saxifraga arguta* Don. Characteristic crane-flies included *Prionocera primoveris* Alexander, *Tipula (Oreomyza) absaroka* Alexander, *Erioptera (Ilisia) rainieria* Alexander, and others. It should be observed that there is a marked resemblance between this station and the Emerald Pool Station, Yellowstone (Alexander, 1943: 721-722); there the dominant heath was a *Ledum* while here the latter was replaced by the three genera listed above. Labelled "Cascade Trail."

5. Jenny and Leigh Lakes; altitude 6,780-6,870 feet; July 3, 4, 6, 10, 12, 1941; Jenny Lake partly repeated in 1942. Collections made along small mountain streams flowing into these lakes. Approximately a half dozen such streams flow down the eastern slopes of the St. John Range into the west side of Jenny Lake; several other similar streams flow from the foothills of Rockchuck Peak at the northern end of the St. John Range northward into the western arm of Leigh Lake. Some of the streams are presumably temporary, fed by the melting snows from the slopes above, but others are unquestionably permanent. The largest of these is Cascade Creek, described under Station 3. In such places as the above, the evergreen forest cover is more boreal in aspect, kinds and number than on the opposite shore of Jenny Lake, the lodgepole pine being replaced chiefly by alpine fir, Engelmann spruce and whitebark pine. Characteristic shrubs include *Alnus tenuifolia*, *Ribes lacustre*, *Sorbus scopulina*, *Rubus parviflorus*, and *Acer glabrum*. Characteristic herbs of the area are *Equisetum arvense*, *Streptopus amplexifolius* (L) DC, *Mitella pentandra*, *Saxifraga arguta* and *Heracleum lanatum*. Some of the more noteworthy Tipulidae of this habitat were *Tipula (Bellardina) jepsoni* sp. nov., *Pedicia (Triclyphona) degenerata* (Alexander), *Dicranota (Dicranota) tetonica* sp. nov., *Ula paupera* Osten Sacken, *Austrolimnophila badia* (Doane), *Limnophila tetonica* sp. nov., *Gonomyia (Idiocera) shannoni* Alexander, *Erioptera (Empeda) tristimonia* Alexander, *Erioptera (Psiloconopa) aperta* (Coquillett), and various species of *Ormosia*, as *O. albertensis* Alexander, *O. dedita* Alexander and *O. hallahani* Alexander. Labelled "Jenny Lake, Leigh Lake."

6. Twogwotee Pass, Teton National Forest; altitude 9,650 feet; July 9, 1942. This single day's collecting provided the best high-altitude material

found in the area. Close to the summit of the pass on this date, numerous masses of snow and ice persisted and conditions were very definitely those of early spring. A great similarity was noted between this station and the one at a slightly lower altitude and earlier date reported at Sylvan Lake, Yellowstone, altitude 8,000 feet, June 21, 1941, as previously described (Alexander, 1943: 720). At the present station, *Caltha rotundifolia* (Huth.) Greene, was in full bloom and many were in full flower while actually protruding through masses of snow; also in full flower were *Trollius albiflorus* (Gray) Rydb., and *Ranunculus eximius* Greene. The forest cover consisted principally of alpine fir and Engelmann spruce, with some limber pine, *Pinus flexilis* James. Great thickets of willow and adjoining wet areas produced many crane-flies. Other excellent collecting was found by sweeping along the margins of small mountain streams close to the pass. Some of the more noteworthy Tipulidae of this place and date included *Tipula* (*Yamatotipula*) *spemax* Osten Sacken, *T. (Arctotipula) twogwoteana* sp. nov., *T. (Oreomyza) absaroka* Alexander, *T. (O.) pseudotruncorum* Alexander, *Ornithodes harrimani* Coquillett, *Molophilus rostriferus* Alexander, and various species of *Ormosia*, as *O. absaroka* Alexander and *O. paradisea* Alexander. It seems certain that this particular station will well repay further collecting at a later seasonal date. A very few additional specimens from here were taken by Mr. and Mrs. Sperry, and by Professor G. F. Knowlton and Mr. H. F. Thornley, the last on September 13, 1941. Labelled "Twogwotee Pass."

I wish to express my deepest thanks to Mrs. Alexander, and to Mr. and Mrs. Harrison and Mr. and Mrs. Sperry, for continued aid in collecting these rich materials in the family. Further acknowledgements of kindly aid and advice are extended to the Park Naturalist, Mr. Carl E. Jepson, and the Ranger Naturalist, Mr. Willis T. Smith, of Ogden, Utah. No one could be more kindly and efficient than these gentlemen and their friendly co-operation is gratefully acknowledged.

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Systematic Account

PTYCHOPTERIDAE

Ptychoptera lenis coloradensis Alexander, 1937.—Twogwotee Pass, Station 6; 9,650 ft., July 9, 1942.

Ptychoptera pendula Alexander, 1937.—Arizona Creek, Station 1; 6,790 ft., July 1-5, 1941; July 4, 1942; Moran bog, Station 2, 6,800 ft., July 5, 1941.

Bittacomorpha clavipes (Fabricius, 1781).—Pilgrim Creek, near Moran, 6,800 ft., in wet swales, July 5, 1942.

TRICHOCERIDAE

Trichocera saltator (Harris, 1782) (*gracilis* Walker, 1848).—Twogwotee Pass, Station 6; 9,650 ft., July 9, 1942.

Trichocera tetonensis sp. nov.—General coloration blackish gray, the praescutum without stripes; knobs of halteres brownish black; legs brownish black to black; wings with a weak brownish tinge, sparsely patterned with darker, including a more distinct cloud over the anterior cord; male hypopygium with the bridge of the basistyles complete; dististyle on mesal face with a flattened compressed blade; dense curved setulae on mesal face of dististyle beyond the marginal blade.

♂. Length, about 6 mm.; wing, 7 mm.; antenna, about 3 mm.

Rostrum and palpi black. Antennae (male) approximately one-half the length of body, brownish black, the outer segments paling to whitish. Head dark brownish gray.

Pronotum brownish gray. Mesonotum darker blackish gray, especially the praescutum and scutum; praescutum without differentiated pattern; scutellum and postnotum clearer gray. Pleura black, sparsely pruinose. Halteres relatively long, stem obscure yellow, knob brownish black. Legs with the coxae dark brown; trochanters obscure yellow; remainder of legs brownish black to black. Wings (Fig. 1) with a weak brownish tinge, the prearcular and basal costal fields more whitened; stigma faintly darkened, lying distad of vein R_2 ; a distinct pale brown cloud over anterior cord; cell Cu_1 and posterior cord somewhat less evidently clouded; veins dark brown, paler in the brightened portions. Venation: Sc_1 ending shortly before level of R_2 , Sc_2

at near one-fifth the length of R_5 ; R_{2+3+4} about one-fourth longer than R_{2+3} ; cell M_1 a little longer than its petiole; $m-cu$ shortly before fork of M_{3+4} ; vein 2nd A angularly bent, its distal portion slightly sinuous.

Abdomen, including hypopygium, black. Male hypopygium (Fig. 2) with the bridge of the basistyles, b , (so-called coxal bridge) complete, at point of union of the lobes produced caudad into a low compressed point. Dististyle, d , elongate, on mesal margin at near one-third the length with a flattened-compressed lobe or blade that is provided with setae on both faces, about fifteen longer setae on upper face, somewhat fewer on lower surface; style beyond the blade a little expanded, with scattered elongate setae at apex and on outer surface; mesal margin as far basad as the blade with short, abundant, curved setulae. Gonapophyses, g , appearing as relatively broad, elongate, flattened blades.



Fig. 1. *Trichocera tetonensis* sp. nov.; venation.

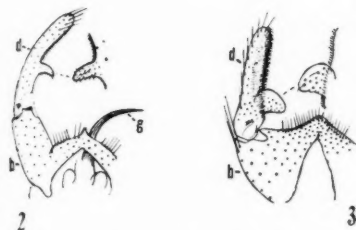


Fig. 2. *Trichocera tetonensis* sp. nov.; male hypopygium.

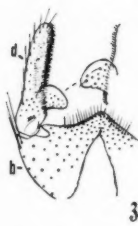


Fig. 3. *Trichocera garretti* Alexander; male hypopygium. (Symbols: b , basistyle; d , dististyle; g , gonapophysis.)

Holotype, ♂, Hidden Falls, Station 3, 6,900 ft., July 8, 1942 (Alexander).

The most similar species is *Trichocera garretti* Alexander, 1927, with a wide distribution in southern Canada and the northern United States (Idaho, Utah). This latter differs especially in the structure of the male hypopygium (Fig. 3). Here the bridge of the basistyles, b , is much larger and more extensive, involving the entire mesal face of the basistyle, completely fused at the midline and here provided with very abundant long pale setae. Dististyle, d , with the blade of mesal face much broader, semicircular in outline, the convexly rounded outer margin without setae; setulae of mesal face of style longer and much more numerous, forming an elongate band from near the apex extending basad to beyond the blade of the style, as illustrated.

TIPULIDAE

TIPULINAE

Prionocera primoveris Alexander, 1943.—Moran bog, 6,800 ft., July 5, 1941; Cascade Trail, Station 4, 8,200 ft., July 9, 1941; Twogwottee Pass, Station 6, 9,650 ft., July 9, 1942, the latter part of the type series.

Nephrotoma ferruginea (Fabricius, 1805).—Jenny Lake, near camp, 6,780 ft., July 1, 1941.

Nephrotoma lugens erythrophrys (Williston, 1893).—Twogwotee Pass, 9,650 ft., July 9, 1942 (M. M. A.).

Tipula (Bellardina) commiscibilis Doane, 1912 (*contaminata* Doane, 1901).—Jackson, Wyoming, August 17, 1941 (J. L. & G. H. Sperry).

Tipula (Bellardina) jepsoni sp. nov.—Allied to *faustina*; antennal flagellum brownish black to black; mesonotal praescutum light gray, with four dark gray stripes that are narrowly bordered by brownish black; interspaces with conspicuous setigerous punctures; wings creamy yellow, marbled with pale grayish brown and darker brown; *Rs* long, from one-half to two-thirds longer than *m-cu*; petiole of cell *M*₁ short, less than one-half *m*; male hypopygium with the ninth tergite produced into a glabrous blackened tooth on either side of midline; setae of tergal lobes relatively short, black, from simple punctures; outer dististyle unusually large and complex, with about four lobes or blades, two of which are provided with dense and abundant black setae.

♂. Length, about 22 mm.; wing, 21.5 mm.; antenna, about 3.8 mm.

♀. Length, about 29 mm.; wing, 24 mm.; antenna, about 4 mm.

Frontal prolongation of head relatively short, gray above, more infuscated on sides; palpi black. Antennae subequal in length in the two sexes; scape brownish yellow, more darkened distally; pedicel yellow; flagellum brownish black to black; flagellar segments with basal enlargements poorly developed; longest verticils much exceeding the segments. Head gray, with a conspicuous median, dark brown stripe; posterior vertex behind eyes less distinctly infuscated.

Pronotum broadly dark brown medially, with a capillary pale central vitta, the sides of sclerite paling to yellow, sparsely pruinose. Mesonotal praescutum with the restricted ground color light gray, with conspicuous brown setigerous punctures; four dark gray stripes that are narrowly bordered by brownish black, the median dark line broader on cephalic half, becoming very narrow to subobsolete behind; humeral and lateral portions of praescutum more or less distinctly infuscated; scutum with median portion brownish gray, each lobe with two dark gray areas that are narrowly bordered by dark brown; scutellum gray, with a capillary dark brown median line, this obsolete on caudal portion; mediotergite light gray on cephalic two-thirds, darker gray behind, with a capillary brown median vitta and poorly indicated brown clouds on either side of basal half of disk; pleurotergite gray, the katapleurotergite abruptly yellow pollinose. Pleura with the broad dorsopleural region light yellow; remainder of pleura dark gray, variegated with lighter gray on the dorsal sternopleurite and the more posterior ventral sclerites. Halteres dark brown, the base of stem and apex of knob slightly more brightened. Legs with the coxae gray, the bases of fore pair more infuscated, of the middle pair less extensively so; trochanters brownish gray; femora yellow to reddish yellow, the tips rather broadly and conspicuously blackened, the amount subequal on all legs; tibiae reddish brown, the tips more narrowly blackened; tarsi black,

the basitarsi somewhat paler on proximal portions; tooth of claws (male) broad but acute. Wings (Fig. 4) with the ground color creamy yellow, conspicuously marbled with pale grayish brown and darker brown; darkest areas relatively extensive, much more so than in *faustina*, especially the post-arcular darkening; area at anterior cord virtually confluent with stigma; yellow band beyond cord wide; outer two-fifths of cell R_5 pale; darkened area in cell Cu distinct, subtended by yellow ground areas. Venation: R_s long, from about one-half to two-thirds longer than $m-cu$; petiole of cell M_1 short, less than one-half m ; $m-cu$ slightly less oblique than in *faustina*.

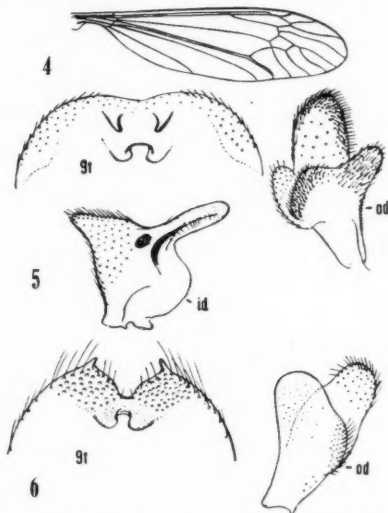


Fig. 4. *Tipula* (Bellardina) *jepsoni* sp. nov.; venation.

Fig. 5. *Tipula* (Bellardina) *jepsoni* sp. nov.; male hypopygium.

Fig. 6. *Tipula* (Bellardina) *faustina* Alexander; male hypopygium. (Symbols: *id*, inner dististyle; *od*, outer dististyle; *t*, tergite.)

Abdomen with basal tergite brownish yellow, darker and more pruinose on posterior portion; succeeding tergites reddish or reddish yellow, the lateral borders gray, narrowly bordered internally by dark brown, on the outer segments this latter becoming more extensive and conspicuous; basal sternites similarly reddish brown; outer segments, including hypopygium, more uniform brownish black. In female, subterminal segments more opaque black, pruinose; ovipositor with cerci long and straight, more than twice the length of the hypovalvae, their ventral margin fringed with long pale setae. Male hypopygium (Fig. 5) with the tergite, *9t*, somewhat as in *faustina*; tergite transverse, with a gentle caudal emargination; on either side with a slender glabrous black tooth, which in slide mounts are bent cephalad; on the ventral side of tergite with a broad depressed plate that is notched at apex to produce two obtuse lobes; setae of tergite relatively short, black, from small simple punctures. Outer dististyle, *od*, unusually complex, on a slide mount appearing about as figured; about four lobes and blades, of which two are provided with unusually abundant and dense black setae. Inner dististyle, *id*, with the sensory area consisting of only eight or nine pegs. Notch of ninth sternite

very shallow, its margin blackened and microscopically corrugated or roughened; no modified flange at base of dististyles.

In *faustina* (Fig. 6), the ninth tergite, *9t*, narrows outwardly, its caudal margin with an irregular V-shaped notch, the lobes thus formed terminating in slender, sparsely hairy lobules; surface of tergal lobes provided with abundant long pale setae from conspicuous punctures to produce a roughened appearance; ventral surface of tergite with two very broad, obtuse, darkened lobes that are separated from one another only by a narrow circular notch; ventral surface of tergal lobes with scattered transverse groups of from four to six small setulae, appearing as microscopic rows or bunches. Outer dististyle, *od*, relatively large but comparatively simple, with only two or three lobes, the vestiture relatively pale. Inner dististyle with the posterior portion of main body relatively stout. Sternal tube unusually short and broad.

Holotype ♂, Jenny Lake, Station 5, 6,780 ft., July 4, 1941 (Alexander).
Allotopotype, ♀ caught with the male but not mating, pinned on same pin.
Paratopotype, 1 ♂, July 6, 1941 (Alexander).

I am very pleased to name this handsome crane-fly in honor of the Park Naturalist of the Grand Teton National Park, Mr. Carl E. Jepson. All of the type specimens were swept from rich herbage close to the margin of a large stream just north of Cascade Creek. The species is closest to *Tipula* (*Bellardina*) *faustina* Alexander, 1941, which differs especially in the venation and pattern of the wings, and in the structure of the male hypopygium, as compared above. In the subgenus *Bellardina* Edwards, 1931, there are more than a dozen species in the Rocky Mountain and Pacific Coast areas, all being large and unusually handsome flies.

Tipula (*Yamatotipula*) *albocaudata* Doane, 1901.—Arizona Creek, 6,790 ft., July 1, 1941.

Tipula (*Yamatotipula*) *colteri* Alexander, 1943.—Twogwotee Pass, Station 6, 9,650 ft., July 9, 1942.

Tipula (*Yamatotipula*) *continentalis* Alexander, 1941.—Cascade Trail, Station 4, 8,200 ft., July 9, 1941.

Tipula (*Yamatotipula*) *spernax* Osten Sacken, 1877.—Twogwotee Pass, 9,650 ft., July 9, 1942; several swept from willow thickets.

Tipula (*Yamatotipula*) *sulphurea jacksonensis* subsp. nov.

♂. Length, about 13 mm.; wing, 11.5 mm.; antenna, about 4.5 mm.

♀. Length, about 14-15 mm.; wing, 12 mm.

Differs from typical *sulphurea* in coloration and in slight structural details. Frontal prolongation of head above gray, with a narrow, obscure yellow, median vitta; sides of prolongation more reddish yellow; nasus conspicuous, especially in female, tufted with long yellow setae. Antennae black, with only the base of scape slightly reddened; first flagellar segment shorter than in *sulphurea*. Head gray to blue gray, with a narrow brown median vitta.

Praescutal stripes more clearly defined and contrasting with the ground; scutellum conspicuously infuscated, especially at base; postnotum clear light

gray, more darkened posteriorly, the lateral border of mediotergite and kateploretergite light yellow, anapleurotergite darkened. Legs with the apices of femora broadly and conspicuously blackened, on the fore legs including the distal half or approximately so, on the remaining legs somewhat narrower; tibiae brown, with blackened tips; tarsi black. Wings with the stigma darker brown and more conspicuous; a more or less distinctly darkened seam along vein *Cu*, in both cells *M* and *Cu*₁. Abdomen with the sublateral black tergal stripes broader and more conspicuous, leaving broad lateral borders; mid-dorsal tergal stripe narrower but very striking.

Holotype, ♂, Moran bog, Station 2, 6,800 ft., July 5, 1941 (*C. P. Alexander*). *Allotopotype*, ♀ pinned with type. *Paratopotypes*, 1 ♂, 3 ♀ ♀.

In its general appearance, the present fly is rather different from the typical form but upon a careful analysis proves to be nothing more than a race of the more eastern and northern *sulphurea* Doane, 1901. The almost uniformly blackened antennae and the increase in amount of gray color on the thorax provide the most evident characters for the separation of this race.

Tipula (Tipula) spenceriana hardyi Alexander, 1943.—Moran, August 7-23, 1941 (*J. L. & G. H. Sperry*).

Tipula (Tipula) pendulifera Alexander, 1919.—Moran, in wet areas, August 26-27, 1942 (*J. L. & G. H. Sperry*). Known hitherto only from Colorado and Alberta. Very recently discovered in Quebec (La Ferme, in late August, *A. Robert*); not hitherto recorded from northeastern North America.

Tipula (Arctotipula) twogwoteeana sp. nov.—General coloration of thoracic notum gray, the praescutum with four stripes that are bordered with dark brown; antennae very short; head and mesothorax with unusually long and abundant black setae; halteres brownish black; legs with femora brown, the tips blackened; wings pale brown or brownish gray, variegated with darker brown and cream-colored areas, the latter including incomplete bands at origin of *Rs* and beyond the stigma; *Rs* gently curved, only a little longer than *m-cu*; cell 1st *M*₅ small; petiole of cell *M*₁ long; abdomen dark gray, the caudal and lateral borders of the segments yellow; ovipositor with short compressed cerci, their tips obtusely rounded.

♀. Length, about 16 mm.; wing, 16 mm.; antenna, about 2.2 mm.

Frontal prolongation of head relatively short, dark gray, conspicuously clothed with long black setae; nasus conspicuous; palpi black, very sparsely pruinose. Antennae (female) very short, black, the basal segments sparsely pruinose; flagellar segments with basal enlargements poorly indicated, verticils long and conspicuous. Head dark brownish gray, with conspicuous erect setae, especially conspicuous surrounding the antennal fossae and on the conspicuous genae; vertical tubercle undeveloped; anterior vertex broad, nearly four times the diameter of scape.

Pronotum dark gray, variegated with lighter gray, the sides with conspicuous erect setae. Mesonotal praescutum with the ground color gray, with four stripes, the intermediate pair more brownish, narrowly bordered by dark brown, the double median margin broad and conspicuous; lateral praescutal

stripes with their restricted centers dark gray, the borders brown; interspaces and lateral borders with conspicuous long black setae; scutum dark gray medially, the lobes somewhat lighter gray, with poorly defined darker central areas; elongate setae of scutum relatively restricted, more numerous along mesal edges of lobes behind the suture and on lateral portions of sclerite; scutellum dark plumbeous gray, the parascutella more infuscated; mediotergite short, light gray, with a darker median stripe, the surface of sclerite on anterior two-thirds with very conspicuous erect setae. Pleura and pleurotergite gray, the mesepisternum, including both anepisternum and sternopleurite, with conspicuous black setae, as in the subgenus; dorsopleural region weakly infuscated. Halteres brownish black, the extreme base of stem brightened. Legs with coxae light gray, clothed with abundant elongate, chiefly pale setae; trochanters dark gray; femora brown, the tips blackened, somewhat more extensively so on the fore femora; tibiae dark brown, the tips more blackened; tarsi black; legs relatively short and stout (female). Wings (Fig. 7) with



Fig. 7. *Tipula (Arctotipula) two-gwoteecana* sp. nov.; venation.

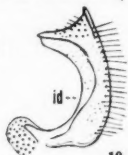


Fig. 8. *Tipula (Arctotipula) two-gwoteecana* sp. nov.; ovipositor, lateral.



Fig. 9. *Tipula (Vestiplex) bali-opteroides* sp. nov.; male hypopygium.

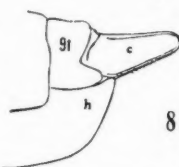


Fig. 10. *Tipula (Vestiplex) bali-optera* Loew; male hypopygium.

(Symbols: c, cercus; h, hypovalva; id, inner dististyle; t, tergite.)

the ground color pale brown or brownish gray, very restrictedly patterned with darker brown and with somewhat more extensive cream-colored areas; the darkest areas include the stigma and confluent areas over anterior cord and at origin of R_s ; the paler ground is somewhat more intense and conspicuous in outer radial field and as areas in cells M and Cu on either side of vein Cu ; the cream-colored markings are most conspicuous as a narrow post-stigmal band extending from costa into cell R_5 and as a more conspicuous oblique band before origin of R_s , extending from costa to vein Cu near outer ends of cells R and M ; further small pale areas in extreme outer end of cell R_5 , in vicinity of vein M_{3+4} , in basal half of cell Cu and in margins of anal cells on either side of vein $2nd\ A$; prearcular field deeper yellow. Macrotrichia of veins extremely reduced in number, as in the subgenus, beyond the cord with only about three or four very scattered trichia over the length of distal section of R_{4+5} ; squama with one or two setae. Venation: R_s gently arcuated, only a little longer than $m-cu$; R_{1+2} entire; cell $1st\ M_2$ small, pentagonal; petiole of cell M_1 long, about three-fifths the length of the cell or approximately three times m ; $m-cu$ on M_4 some distance beyond base; cell $2nd\ A$ wide.

Abdomen dark gray, the lateral and caudal borders of the segments narrow-

ly pale yellow; tergites with vestiture much reduced, with scattered small black setae only; sternites with vestiture similarly inconspicuous, appearing as longer pale scattered setae; genital segment brownish yellow. Ovipositor (Fig 8) with cerci, c, short, compressed, the tips obtuse, margins smooth; hypovalvae, h, very short and blunt; lateral border of ninth tergite produced slightly caudad as a small lobe over the base of cercus.

Holotype, ♀, Twogwotee Pass, Station 6, 9,650 ft., July 9, 1942 (C. P. Alexander); ovipositing in wet earth at margin of small mountain torrent.

The present fly is readily distinguished from other regional members of the subgenus by the handsomely patterned wings. The fly bears a general resemblance to *Tipula* (*Oreomyza*) *pseudotruncorum* Alexander, with which it was associated in nature, but the subgeneric characters readily separate the two flies. It should be emphasized that such characters include the abundant body setae of *Arctotipula* as contrasted with the more nearly glabrous condition in *Oreomyza*, this condition being well shown in the two species of *Tipula* here discussed.

Tipula (*Vestiplex*) *baliopteroides* sp. nov.—Allied to *balioptera*; basal flagellar segments more or less bicolored; wing pattern whitish subhyaline and restricted dark brown on a pale brownish gray ground; abdomen chiefly yellow, the tergites trivittate with dark brown; male hypopygium with a very conspicuous blackened tergal saucer, armed at anterior and posterior angles with strong spines, with a further more or less developed discal spine near base of median notch; inner dististyle stout-stemmed.

♂. Length, about 13-15 mm.; wing, 14-16 mm.; antenna, about 5 mm.

Frontal prolongation of head dark brown above, sparsely pruinose, paler beneath; nasus elongate; palpi brown, the terminal segment passing into black. Antennae with proximal three segments yellow, the succeeding segments usually bicolored, the basal swelling black, the remainder yellow, at about the fifth to seventh flagellar segments the color becoming uniformly dark; in one paratype, the bicolorous nature is lost almost on the second or third segment; flagellar segments rather strongly incised. Head gray, clearer in front, with a conspicuous brown longitudinal line extending from the low vertical tubercle to the occiput, narrowed behind.

Pronotum dark gray. Mesonotal praescutum gray, with four slightly differentiated clearer gray stripes that are conspicuously margined with brown; scutal lobes each with two similar brown ringed areas; posterior sclerites of notum gray, with a median brown vitta. Pleura chiefly gray, the dorsopleural membrane yellow; vague patterns of paler gray on the dorsal sternopleurite in some specimens. Halteres with stem obscure yellow, knob infuscated. Legs with the coxae pale, gray pruinose; trochanters yellow; femora obscure yellow, the tips brownish black, the amount subequal on all legs; tibiae and tarsi obscure yellow, the terminal tarsal segments darkened. Wings with the ground pale brownish gray, variegated by slightly darker brown and more extensive whitish subhyaline areas; the darker pattern includes the stigma, adjoining portion of anterior cord and a small spot over origin of *Rs*; the pale marks include a broad band beyond stigma, extending from costa to cell 1st *M*₂, including

the bases of cells of the outer radial field; the white obliterative band at cord is especially conspicuous from outer end of cell *R*, across 1st *M*₂ into base of *M*₃; other pale areas at near two-thirds cell *M* and near basal third of cells *Cu* and 1st *A*; no darkened area at arculus nor any whitening in cells immediately beyond; prearcular and costal fields clearer yellow; veins brown, more brownish yellow in the brightened fields. Venation: *R*_s long, nearly three times *m-cu*; *R*₁₊₂ long; inner end of cell 1st *M*₂ pointed; petiole of cell *M*₁ nearly twice *m*.

Basal abdominal tergite brownish yellow, sparsely pruinose, restrictedly patterned with darker brown; succeeding tergites bright yellow with three dark brown stripes that are more or less interrupted at the posterior borders of the segments; sublateral stripes widened posteriorly; lateral tergal margins pale; sternites yellow, the outer segments more infuscated and pruinose; tergites eight and nine, and, in cases, tergite seven, more darkened; outer portions of hypopygium (Fig. 9) with the tergal saucer, 9t, heavily blackened and very conspicuous, its greatest length nearly equal to the maximum width, narrowed anteriorly; posterior angles produced caudad into strong horns, the anterior angles similarly produced, these horns directed chiefly cephalad; margin of saucer with further spinous points and denticles; caudal margin with a quadrate notch, at or near base of which arises a single median horn or spine, as in *balioptera*; in the type, as figured, the horn appears to lie very close to the base of the notch, in other specimens somewhat more removed from the margin. Outer dististyle narrower than in *balioptera*. Inner dististyle, *id*, with the stem much stouter and broader, the fringe of yellow setae sparse and chiefly confined to the distal portion. I have shown the inner dististyle (Fig. 10, *id*) of *balioptera* for comparison; here the stem is narrower, the entire outer surface with abundant long delicate pale setae from very pale and inconspicuous punctures.

Holotype, ♂, Pilgrim Creek, near Moran, 6,800 ft., July 5, 1942 (*M. M. Alexander*). *Paratypes*, 1 ♂, Arizona Creek, Station 1, 6,790 ft., July 8, 1941 (*C. P. Alexander*); 1 ♂, Gothic, Colorado, 9,500 ft., July 1, 1934 (*C. P. Alexander*).

The present fly is readily distinguished from the more northern, subarctic *Tipula* (*Vestiplex*) *balioptera* Loew, 1863, by the hypopygial characters, especially the details of the tergal saucer and the inner dististyle. The latter species is known from Saskatchewan and Alberta, the types being from English River (now Churchill River), Saskatchewan, at near 56° N.Lat., and from the then Russian America, all collected by Robert Kennicott.

Tipula (*Schummelia*) *subtenuicornis* Doane, 1901.—Jenny Lake, 6,780 ft., July 4-5, 1941; Leigh Lake, 6,870 ft., July 10-12, 1941; Hidden Falls, 7,000 ft., July 8, 1942; Death Canyon, 7,800 ft., July 14, 1941.

Tipula (*Oreomyza*) *absaroka* Alexander, 1943.—Cascade Trail, Station 4, 8,200 ft., July 9, 1941; Twogwotee Pass, Station 6, 9,650 ft., July 9, 1942; part of the type material (Alexander, 1943: 729).

Tipula (*Oreomyza*) *alia* Doane, 1911.—A single female, Death Canyon,

7,000 ft., July 14, 1941. In this, R_5 is longer than in any other specimen that I have seen but the identification seems correct.

Tipula (Oreomyza) fundata sp. nov.—Belongs to the *borealis* or *unca* group; most similar to *coloradensis* and *criddleii*; antennal flagellum uniformly blackened; mesonotum gray, the praescutum and scutum conspicuously patterned; tips of femora narrowly blackened; wing pattern only weakly developed; abdomen with a conspicuous median, dark brown stripe that becomes obsolete beyond segment six; male hypopygium with the lateral appendage bearing a pair of blackened spinous points; gonapophyses strong, terminating in a spatulate head.

♂. Length, about 10-13 mm.; wing, 11-15 mm; antenna, about 4-5.2 mm.

♀. Length, about 15 mm.; wing, 14 mm.

Frontal prolongation of head pale, sparsely pruinose; nasus elongate, black; palpi black. Antennae of moderate length; scape and pedicel yellow, flagellum black. Head gray, paler gray on front and anterior vertex.

Pronotal scutum brownish gray, with a narrow median infuscation; scutellum yellow. Mesonotal praescutum with the ground color gray, the stripes barely indicated, best marked by brown borders that form an irregular pattern, the intermediates widened on anterior portion, very narrow behind, the posterior ends recurved; lateral brown stripes forming strongly curved hook-shaped lines; scutum gray, the lobes with scarcely indicated darker gray areas that are narrowly bordered by pale brown; scutellum and mediotergite gray, with a vague capillary median darkening. Pleura extensively gray, the posterior sclerites, including the katapleurotergite, more yellow; dorsopleural membrane buffy yellow. Halteres with stem obscure yellow, knob brownish black. Legs with the coxae brownish gray; trochanters yellow; femora yellow, the tips rather narrowly but very conspicuously blackened, the amount subequal on all legs; tibiae and basitarsi obscure yellow, the tips very narrowly infuscated; outer tarsal segments blackened. Wings with the ground color pale brown, restrictedly patterned with darker brown and whitish subhyaline; prearcular field and cell Sc much clearer yellow; stigma dark brown; small darker brown areas at origin of R_5 and over anterior cord; somewhat paler clouds in outer radial field, outer end of cell $1st\ M_2$ and in cells M and Cu , the two latter alternating with whitish subhyaline spots; whitish post-stigmal band passing through cell $1st\ M_2$ into bases of adjoining cells; outer end of cell R_5 slightly brightened; veins brownish black, yellow in the flavous areas. Venation: R_5 variable in length, from approximately twice to about three times $m-cu$.

Abdominal tergites yellow, the first more infuscated; a conspicuous, dark brown median stripe, ending at about segment six, narrowly interrupted by pale caudal borders of the segments; sternites and subterminal tergites more yellowish; ninth segment and eighth sternite chiefly black; genital shield black; cerci long and slender. Male hypopygium (Fig. 11) relatively large. Ninth tergite, $9t$, with the caudal margin truncate, with a small median notch; each lobe with a conspicuous outer horn on ventral surface, this directed chiefly caudad. Outer dististyle, od , truncated at apex. Inner dististyle, id , with

the setae of dorsal crest relatively inconspicuous, excepting a group or pencil immediately back of the beak. Lateral appendage, *la*, with two blackened teeth or denticles, as in *coloradensis* and *criddlei*; pendulous lobe moderately elongate, broad at base. Gonapophyses, *g*, strongly developed, broad at base, much narrowed before a conspicuous dilated apical spatula. Eighth sternite with caudal margin weakly biemarginate to form three blunt lobes that are fringed with abundant long pale setae, those of the central lobe longer and more conspicuous.

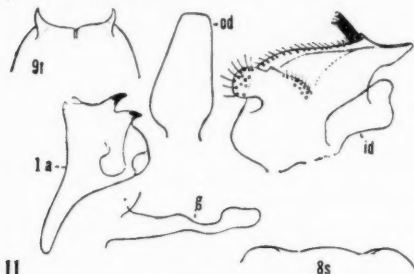


Fig. 11. *Tipula (Oreomyza) fundata* sp. nov.; male hypopygium.

(Symbols: *g*, gonapophysis; *id*, inner dististyle; *la*, lateral appendage; *od*, outer dististyle; *s*, sternite; *l*, tergite.)

Holotype, ♂, Buffalo Creek, below Twogwotee Pass, 8,000 ft., July 9, 1942 (C. P. Alexander). *Allotype*, ♀, Richel Lodge, Montana, August 20, 1942, (J. L. & G. H. Sperry). *Paratypes*, 1 ♂, with the allotype; 1 ♂, Plateau of Beartooth Mts., Wyoming, 10,000 ft., July 29, 1942 (J. L. & G. H. Sperry); ♂♂, Arizona Creek, Station 1, 6,790 ft., July 4, 1941 (C. P. Alexander); ♂♂, Moran bog, Station 2, 6,800 ft., July 2-5, 1941 (M. M. Alexander); ♂♂, Death Canyon, 7,800 ft., July 14, 1941 (C. P. Alexander); 1 ♂, Twogwotee Pass, 9,650 ft., July 24, 1942 (J. L. & G. H. Sperry).

The two species with which the present fly requires comparison are *Tipula (Oreomyza) coloradensis* Doane, 1911, and *T. (O.) criddlei* Dietz, 1914. Both of these have the lateral appendage of the male hypopygium having two upper teeth or points, much as in the present fly. The former fly is described as having the entire abdomen yellowish brown, darker posteriorly, without the conspicuous central darkened tergal stripe; ovipositor with the cerci long and slender, as in the present fly. The latter species, described from Manitoba, has the abdominal pattern much as in the new form; ovipositor with unusually short valves, the cerci and hypovalvae being of equal length. Both of these species are described and figured as having the gonapophyses slender, with the apical portion curved into a sickle, not at all as in the insect here defined.

Tipula (Oreomyza) gaspensis Alexander, 1929.—This small fly had been known only from eastern Canada. It was found commonly at various stations throughout the Tetons. Arizona Creek, 6,790 ft., July 8, 1941; Moran bog, 6,800 ft., July 2, 1941; Hidden Falls, 7,000 ft., July 4, 1941; Jenny Lake, Station 5, 6,790 ft., July 6, 1941; Leigh Lake, Station 5, 6,870 ft., July 12, 1941; Indian Paintbrush Canyon, 8,000 ft., July 13, 1941; Death Canyon, 7,800 ft., July 14, 1941. As was the case with Quebec specimens, in this material *Rs* similarly varies in length within rather surprisingly wide limits.

Tipula (Oreomyza) ingrata Dietz, 1914.—Arizona Creek, Station 1, 6,790 ft., July 2, 1941 (M. M. Alexander).

Tipula (Oreomyza) sarta Loew, 1863 (*albonotata* Doane, 1901).—Pilgrim Creek, near Moran, July 25, 1942 (J. L. & G. H. Sperry).

Tipula (Oreomyza) pseudotruncorum Alexander 1920.—General coloration gray, the praescutum yellowish gray with four brownish black stripes, the intermediate pair with an interpolated median dark vitta; antenna short, flagellum uniformly black; head, scutellum and mediotergite with a central brown vitta; knobs of halteres dark brown; femora brownish yellow, the tips narrowly blackened; claws (male) toothed; wings yellowish white, heavily clouded with pale brown and darker brown; R_s long, exceeding twice $m-cu$; R_{1+2} entire; cell 1st M_2 large; petiole of cell M_1 short, subequal to or shorter than m ; abdominal tergites gray, heavily patterned with brown, the posterior borders of the segments yellow; male hypopygium with the beak and outer basal lobe of the inner dististyle heavily blackened; eighth sternite with lateral lobes that bear conspicuous hair tufts.

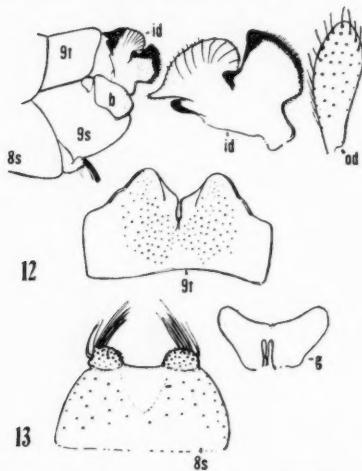
♂. Length, about 14.5-15 mm.; wing, 16-17 mm.; antenna, about 3 mm.

Frontal prolongation of head relatively long, dark gray; nasus very short; palpi black. Antennae (male) short; scape elongate, transversely corrugated; pedicel brown; flagellum uniformly black; flagellar segments short, with basal enlargements feebly developed; verticils longer than the segments; terminal segment reduced to a small thimble-shaped structure. Head gray; vertex infuscated medially; vertical tubercle very low and simple.

Pronotum brownish gray, more infuscated above. Mesonotal praescutum yellowish gray with four brownish black stripes, with a further narrow central vitta, the intermediate three stripes all narrowed behind and connected at the suture; lateral stripes narrow, with slightly paler, more brownish gray centers; humeral region in vicinity of pseudosutural foveae more or less darkened; scutum yellowish gray, each lobe with two brownish gray areas, the more cephalic one much smaller; scutellum and postnotum clearer gray, with a narrow, interrupted median brown vitta. Pleura and pleurotergite clear gray; dorsopleural membrane yellow, conspicuously variegated with brown areas along both the dorsal and ventral edges. Halteres brownish yellow, knobs dark brown. Legs with coxae light gray; trochanters obscure yellow or brownish yellow, the tips narrowly blackened, the amount subequal on all legs; tibiae dark brown, the tips more blackened; tarsi black; claws (male) toothed. Wings with the ground pale yellowish white, heavily clouded with pale brown and with fewer dark brown areas; the darkest clouds include the stigma and a confluent cloud over the anterior cord, origin of R_s , and a spot in bases of cells R and M at arculus; paler brown clouds in distal half of outer radial field, as seams along outer medial veins, most of cell R , and two conspicuous clouds in cells M and Cu , separated from one another by a ground area about opposite origin of R_s ; cell 1st A conspicuously clouded, cell 2nd A virtually clear except for a narrow axillary margin; the creamy areas include a broad, nearly complete band beyond cord, extending from C to the posterior margin

in outer medial field; cells C and Sc; prearcular cells and conspicuous areas in cells M to 1st A; veins dark brown, Sc paler at base. Macrotrichia on outer veins, from R_{4+5} to 2nd A inclusive. Venation: R_s long, exceeding twice $m-cu$; R_{1+2} entire; cell 1st M_2 large, exceeding in length vein M_3 beyond it; petiole of cell M_1 short, subequal to or less than m .

Abdominal tergites gray, clearest laterally, heavily patterned with brown, on the first segment this including a narrow mid-dorsal area; tergite two with a continuous dorsal and interrupted sublateral stripes; succeeding segments with dorsal and sublateral stripes more extensive and becoming confluent; all segments with a more yellowish posterior border, this more distinct and broader on segments four to eight, inclusive; sternites more uniform brownish gray, with conspicuous yellow posterior borders; ninth segment more brownish gray, the posterior margins of both the tergite and sternite more reddish yellow; dististyles chiefly pale. Male hypopygium (Figs. 12, 13) relatively small and of simple structure; ninth tergite entirely separated from ninth sternite; basistyle complete; accessory sclerite small but developed. Ninth tergite, $9t$, generally rectangular in outline, transverse; caudal margin produced into two flattened yellow lobes that are separated from one another at the midline only by a very narrow notch; posterior borders of lobes obliquely truncated, their surface with the setae sparse and very small. Ninth sternite, $9s$, extensive,



Figs. 12, 13. *Tipula (oreomyza) pseudotruncorum* Alexander; male hypopygium.

(Symbols: b, basistyle; g, gonapophysis; id, inner dististyle; od, outer dististyle; s, sternite; t, tergite.)

with a median line of pale membrane, on caudal portion widened to form a V-shaped incision; caudomesal margins of notch with a small lobe on either side, this bearing abundant long yellow setae that virtually fill the whole incision. Basistyle, b, not produced caudally, its outer portion provided with several long setae. Outer dististyle, od , relatively broad and flattened. Inner dististyle, id , with both the beak and the outer basal lobe heavily blackened and unusually short and compact; posterior crest of style thin, pale yellow,

longitudinally striate, its posterior border microscopically erose. Gonapophyses, g, appearing as a pair of very thin, flattened plates. Eighth sternite, $8s$, moderately sheathing, the median area filled with pale membrane; each posterior angle bearing an oval lobe that is completely detached from body of sternite by pale membrane; each lobe bearing numerous strong setae, some of which are grouped into a more conspicuous apical tuft or pencil directed caudad and slightly mesad, more or less decussate across midline with its mate of opposite side.

This rare fly was taken at Twogwotee Pass, Station 6, 9,650 ft., July 9, 1942 (M. M. Alexander). It is most closely related to *Tipula* (*Oreomyza*) *shoshone* Alexander, 1945, and *T. (O.) ternaria* Loew, 1864, both of which it somewhat resembles in general appearance. It is readily told by the nature of the wing pattern and by the structure of the male hypopygium, particularly of the ninth tergite, inner dististyle and eighth sternite. Mrs. Alexander captured these specimens while they were flying high among the spruces on a forested slope not far from a cold mountain torrent. A few others were observed but always so high that they could not be netted. The species had not been figured or adequately described hitherto.

Tipula (*Oreomyza*) *trivittata* laetifica subsp. nov.

♀. Length, about 26 mm.; wing, 20.5 mm.

Close to typical *trivittata* Say, 1823, differing especially in the distribution of the wing pattern which gives the fly a distinctive appearance.

Arctular darkening restricted; dark crossband at near one-third the length of wing widely separated from the brown spot at origin of R_5 ; wing apex only restrictedly darkened, the areas in outer ends of cells R_2 and R_3 solid, in the remaining cells represented only by narrow but conspicuous dark seams to the veins, leaving the central portions of cells R_5 to M_4 , inclusive, white. In typical *trivittata*, these cells are dark with the exception of M_3 which is traversed by the complete white band before the stigma and cord; the other cells, in cases, have restricted pale areas but are not whitened as in the present fly; the dark spot at origin of R_5 is confluent with the dark band at near one-third the wing length.

Holotype, ♀, Jenny Lake, Grand Tetons, 6,780 ft., August 9, 1942 (J. L. & G. H. Sperry).

The discovery of the male sex of the present fly will show whether there are any hypopygial characters to support the distinctions indicated above. I have seen typical *trivittata* from the Black Hills, South Dakota (Harney Peak and vicinity, 6,500 ft., June 15, 1941, Alexander).

Tipula (*Lunatipula*) *bisetosa* percita subsp. nov.

Differs from typical *bisetosa* Doane, 1901, chiefly in minor hypopygial details, especially of the eighth sternite. In the present fly, this shows the cushion between the major lateral setae as transverse, its caudal border truncate or even weakly bilobed, the entire cushion with more abundant setae.

In typical *bisetosa*, the cushion is roughly semicircular in outline, its posterior border evenly rounded to strongly convex, the surface with fewer setae.

Holotype, ♂, Jenny Lake, Grand Tetons, 6,780 ft., August 10, 1942 (*J. L. & G. H. Sperry*). *Allotopotype*, ♀, August 6, 1942. *Paratopotype*, ♂, August 9, 1942 (*Sperry*).

Tipula (Lunatipula) diversa Dietz, 1921.—Jenny Lake, around camp, July 1-9, 1941; a few, flying beneath the evergreens, associated with the much more numerous *pellucida* and *sinistra*.

Tipula (Lunatipula) johannus sp. nov.—Allied to *barbata*; general coloration gray, the praescutum with four narrow brown stripes; capillary dark gray lines on head, scutellum and mediotergite; tips of femora narrowly blackened; wings with a strong brown ground, the obliterative areas at cord and beyond stigma unusually large and conspicuous; abdominal tergites yellow, trivittate with brownish black; sternites with an unusually broad black central stripe; male hypopygium with the lobes of the tergite obliquely truncate; ninth sternite with the lobes large, with conspicuous pencils of long reddish setae; inner dististyle with beak long and slender, outer basal lobe long and narrow, unarmed; eighth sternite with the outer major bristle strongly tuberculate; median sternal plate transverse, its central portion produced into a rounded lobe.

♂. Length, about 12.5 mm.; wing, 12 mm.; antenna, about 3.5 mm.

Frontal prolongation of head dark brown, sparsely pruinose at base above; nasus short but distinct; palpi black. Antennae with scape and pedicel yellow, flagellum black; flagellar segments moderately incised, a little longer than the verticils. Head gray, with a conspicuous black vitta on vertex.

Pronotum gray, with a narrow, dark brown, median dash. Mesonotal praescutum gray with four narrow but conspicuous entire brown stripes; intermediate pair narrow to obsolete at their cephalic ends, widest at near mid-length, separated by a ground vitta of about the same width; a dusky triangular area in humeral region; scutum gray, each lobe with two disconnected dark brownish gray areas; scutellum and mediotergite gray with a capillary black median vitta. Pleura and pleurotergite gray; dorsopleural membrane buffy. Halteres with stem dusky, narrowly yellow at base, knob blackened, its apex a trifle paler. Legs with coxae pale, gray pruinose; trochanters yellow; femora yellow, the tips narrowly blackened, a very little more extensive on fore legs; tibiae yellow, the tips more narrowly infuscated; basitarsi dark brown; remainder of tarsi black; claws (male) toothed. Wings with a strong brownish ground, deeper than in allied species, especially in the cells beyond cord; stigma oval, still darker brown; basad of cord the dark ground is more restricted to the centers of the cells, the vicinity of the veins broadly pale, this including almost all of cell *Cu* and the broad bases of the Anal cells; cells *C* and *Sc* uniformly darkened except at their whitened outer ends, cell *Sc* a little more yellowish; whitish obliterative areas along cord and beyond stigma unusually extensive and conspicuous against the ground, including almost all of cell *R*₁; dark central area of cell *1st A* with a whitish elongate marginal streak; veins dark brown, brownish yellow in the costal and prearcular fields.

Venation: R_s moderately long, more than one-half longer than $m-cu$; R_{1+2} entire; petiole of cell M_1 shorter than m ; cell $1st\ M_2$ relatively long, its outer end pointed.

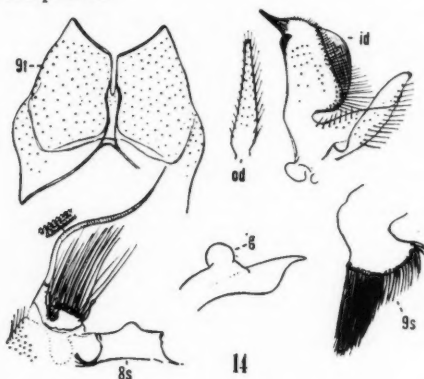


Fig. 14. *Tipula (Lunatipula) johannus* sp. nov.; male hypopygium.

(Symbols: g, gonapophysis; id, inner dististyle; od, outer dististyle; s, sternite; t, tergite.)

Abdominal tergites with first segment gray pruinose; succeeding segments yellow, conspicuously trivittate with brownish black, the mid-dorsal stripe narrowly interrupted by pale caudal borders to the segments; sublateral stripes similarly broken, conspicuously wavy on the more proximal tergites; lateral borders pale; sternites yellow, with an unusually broad and conspicuous black mid-ventral stripe that is only narrowly broken at the incisures; hypopygium brownish yellow. Male hypopygium (Fig. 14) complex, as in the *barbata* subgroup. Ninth tergite, $9t$, with the median incision unusually deep and narrow; lateral lobes obliquely truncate, their outer angles subacute. Ninth sternite, $9s$, with the lobe very conspicuous, transversely elongate-oval, the lower margin with unusually long and conspicuous reddish setae, the inner group longer, more compact and forming a strong brush or pencil. Outer dististyle, od , long and narrow, as in the subgroup. Inner dististyle, id , with the beak long and slender; dorsal crest high, with all portions evenly rounded; outer basal lobe long and slender, twisted, unarmed with teeth or spines. Gonapophyses, g , with the outer sclerotized knobs rounded; inner compressed blades produced into a slender apical point. Eighth sternite, $8s$, with the armature of the outer semi-detached lobes conspicuous; at outer lateral portion a small cylindrical peduncle bearing a single unusually strong and powerful spinous seta, its surface with microscopic tubercles; remaining setae long and conspicuous, their margins fimbriate, those lying closest to the mesal portion of lobe arising from expanded bases; median plate of sclerite sclerotized, transverse, the central portion of the posterior border produced into a rounded lobe.

Holotype, ♂, Jenny Lake, Grand Tetons, 6,790 ft., August 10, 1942 (J. L. & G. H. Sperry).

I am very pleased to name this fly in honor of Mr. John L. Sperry, to whom I am greatly indebted for numerous interesting Western Tipulidae. The fly is allied to *Tipula (Lunatipula) barbata* Doane, 1901, and to *T. (L.)*

subbarbata Alexander, 1927, more particularly to the latter. The structure of the male hypopygium, especially as regards the inner dististyle, is more as in *subbarbata*, but it differs from this latter fly in almost every detail of the hypopygium; as regards the inner style, the present species differs in the more elongate beak, the evenly rounded dorsal crest, and the unarmed outer basal lobe. The shape and armature of the paired lobes of the ninth sternite of the present fly is entirely distinct from those of either of the allied species mentioned.

Tipula (Lunatipula) macrolabis macrolaboides Alexander, 1918.—Pilgrim Creek, Moran, 6,800 ft., July 25, 1942 (J. L. & G. H. Sperry). Jenny Lake, Station 5, 6,780 ft., July 4, 1941; August 8-9, 1942 (Sperry); Hidden Falls, 7,000 ft., July 4, 1941 (W. H. Harrison).

I had considered this fly as being identical with *macrolabis* Loew, 1864, but now believe it represents a distinct race, best differentiated by the unusually narrow arm of the basistyle, at its apex this being only a little wider than the basal portion. In typical *macrolabis*, this blade is distinctly widened into a paddle. From Snodgrass' description and figures of the hypopygium of *spectabilis* Doane, 1901, based on type material from Idaho (Trans. Amer. Ent. Soc., 30:220-221, figs. 156, 158-161; 1904), it is evident that the latter is a synonym of typical *macrolabis*.

Tipula (Lunatipula) pellucida Doane, 1912 (*clara* Doane, 1901).—Shores of Jenny Lake, July 1-5, 1941; String Lake, 6,870 ft., July 7, 1941; Hidden Falls, 6,900 ft., July 4, 1941. This is the commonest crane-fly among the lodgepole pines of the eastern shore of Jenny Lake, often associated with *T. (L.) sinistra* Dietz.

Tipula (Lunatipula) saxemontana Alexander, 1945.—Arizona Creek, Station 1, 6,790 ft., July 2-8, 1941; Pilgrim Creek, Moran, 6,800 ft., July 5, 1942.

Tipula (Lunatipula) sinistra Dietz, 1921.—Jenny Lake, among the lodgepole pines, 6,780 ft., July 1-12, 1941; July 5, 1942, associated with *pellucida*; Hidden Falls, 6,900 ft., July 4, 1941; String Lake, 6,750 ft., July 7, 1941; Leigh Lake, 6,870 ft., July 12, 1941.

Tipula (Lunatipula) splendens Doane, 1901.—Pilgrim Creek, Moran, 6,800 ft., July 5, 1942; Jenny Lake, 6,780 ft., August 8, 1942 (J. L. & G. H. Sperry); Leigh Lake, 6,875 ft., July 12, 1941; Indian Paintbrush Canyon trail, 7,500 ft., July 13, 1941, the last relatively abundant in unusually dry places along the trail; String Lake, 6,870 ft., July 7, 1941, associated with *Limnophila (Phylidorea) adusta* Osten Sacken.

Tipula (Lunatipula) uncinata Doane, 1901.—Pilgrim Creek, near Moran, 6,900 ft., August 9, 1942 (J. L. & G. H. Sperry).

Tipula (Lunatipula) willis-smithi sp. nov.—Size relatively large (wing, male, over 15 mm.); general coloration yellowish gray, the praescutum with three brownish yellow stripes that are narrowly bordered by reddish brown; antennal flagellum black; wings brownish gray, conspicuously patterned with

darker brown, especially evident as a seam over the posterior cord; male hypopygium with the ninth sternite produced caudad into a long conspicuous arm; ninth tergite with caudal border terminating in six blackened teeth.

♂. Length, about 16-17 mm.; wing, 17-18 mm.; antenna, about 4.8-5 mm.

Frontal prolongation of head brownish yellow above, in cases a little darker laterally; nasus short and stout; palpi with proximal segments obscure yellow, the intermediates brownish yellow, the terminal segment black. Antennae with scape and pedicel yellow; first flagellar segment brown, remainder of flagellum black; flagellar segments moderately incised; longest verticils exceeding the segments in length. Head buffy, narrowly gray pruinose on orbits.

Pronotum brownish yellow. Mesonotal praescutum with the interspaces yellowish gray, with three poorly differentiated stripes, these brownish yellow with more reddish brown margins; scutal lobes brownish gray; scutellum

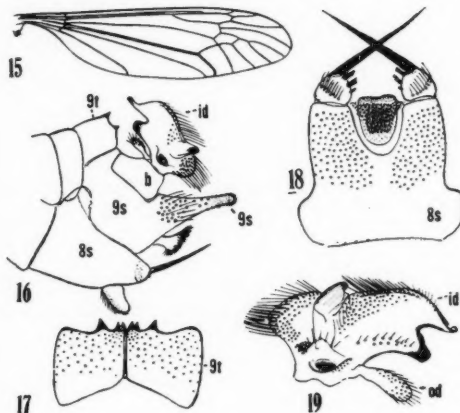


Fig. 15. *Tipula* (*Lunatipula*) *willis-smithi* sp. nov.; venation.

Figs. 16-19. *Tipula* (*Lunatipula*) *willis-smithi* sp. nov.; male hypopygium.

(Symbols: *b*, basistyle; *id*, inner dististyle; *od*, outer dististyle; *s*, sternite; *t*, tergite.)

darker brown; postnotum brownish gray, sparsely pruinose. Pleura light brown or yellowish brown, sparsely pruinose, especially on the mesepisternum. Halteres brownish black, base of stem paler, apex of knob more or less brightened. Legs with coxae brownish yellow; trochanters slightly darker; remainder of legs brown, tarsi passing into black; claws (male) with a conspicuous tooth. Wings (Fig. 15) brownish gray, conspicuously patterned, including a dark brown seam along cord, particularly the posterior cord; less conspicuous brown suffusions in costal field, along *Rs*, broad bases of outer radial field, including the anterior cord, and as seams along veins *Cu* and *2nd A*; outer ends of Anal cells suffused; a very conspicuous whitened obliterative area before the cord and stigma, extending from cell *R*₁, before stigma across cell *1st M*₂ into base of *M*₃, narrowly interrupted at *Rs*; stigma brown, its proximal end more yellowish; a scarcely evident post-stigmal brightening, chiefly in base of cell *R*₂; prearcular field more yellow or brownish yellow; veins brown. Venation:

R_s relatively long, approximately three-fourths longer than $m-cu$; cell $1st\ M_2$ relatively small, pentagonal; petiole of cell M_1 subequal to or a little shorter than m ; $m-cu$ at fork of M_{3+4} .

Basal abdominal tergites yellow, the outer segments more reddish brown, passing into dark brown on outer segments; basal tergite slightly pruinose; tergites with three little-developed brown stripes, broader and more evident on outer segments; basal sternites clear yellow, the outer segments passing into dark brown. Male hypopygium (Figs. 16-19) with both the tergite and basistyle entirely cut off from sternite by sutures. Ninth tergite, $9t$, a transverse plate that is completely divided medially by a furrow; caudal margin of either half heavily blackened and produced into three strong black spinous points, two of which lie more dorsad, the third immediately beneath the more mesial of these, close to midline. Ninth sternite, $9s$, immediately ventrad of basistyle, produced caudad into a long powerful arm that gradually narrows to an obtusely rounded point, the enlarged base with numerous long coarse setae, the distal portion clothed with abundant microscopic setulae; ventrad and mesad of this arm projects caudad a second lobe that is shorter but still very conspicuous, short-stemmed, expanded at apex into a head that is provided with abundant reddish setae, the more dorsal ones longer and more delicate. Outer dististyle, od , a small pale, relatively narrow spatula. Inner dististyle, id , about as figured, the actual beak very slender, blackened, slightly twisted, separated from the shorter and stouter obtuse subapical beak by a rounded notch; outer basal lobe closely applied to main body of style, with a flattened, sclerotized plate lying in the notch; sensory area large, comprised of more than 25 pegs, placed close to base of style. Gonapophyses appearing as long powerful blackened spines. Eighth sternite, $8s$, sheathing, its dorsal-cephalic region strongly produced into a lobe; caudal margin with a deep U-shaped emargination that is filled with membrane in which is suspended a conspicuous subquadrate lobe that is densely covered with microscopic setulae; its lower or ventral surface with a central brush of long reddish setae, the outer or more caudal ones becoming shorter and less conspicuous; lateral lobes of sternite bearing a disconnected plate that is separated from the main body by a complete suture, at apex produced into a powerful black horn, probably composed of fused or fasciculate bristles; at base of this latter with several strong setae, and on mesal face close to base of horn with two smaller hair tufts.

Holotype, ♂, near Pilgrim Creek, Teton National Forest, in woods, 6,800 ft., July 5, 1942 (C. P. Alexander). *Paratype*, ♂, Jenny Lake, Grand Tetons, 6,780 ft., August 10, 1942 (J. L. & G. H. Sperry).

This fine species is dedicated to the Ranger Naturalist, Professor Willis T. Smith, of Ogden, Utah. The general appearance of the male hypopygium suggests species such as *Tipula* (*Lunatipula*) *saxemontana* Alexander, but the actual structure is entirely distinct. In the latter fly it is the basistyle that is produced into an arm whereas in the present fly this structure is a direct prolongation of the ninth sternite, ventrad of the basistyle. The conspicuously patterned wings likewise are distinctive of the present fly.

CYLINDROTOMINAE

Cylindrotoma pallescens Alexander, 1930.—Common in situations described under Station 5; Jenny Lake, 6,780 ft., July 3, 1941; Leigh Lake, 6,870 ft., July 10-12, 1941.

LIMONIINAE

LIMONIINI

Limonia (Limonia) cinctipes (Say, 1823).—Moran, August 7, 1941 (J. L. & G. H. Sperry).

Limonia (Limonia) indigena jacksoni (Alexander, 1917).—Jenny Lake, 6,780 ft., July 4, 1941; Leigh Lake, 6,870 ft., July 10-12, 1941; Indian Paintbrush Canyon, 7,500 ft., July 13, 1941.

Limonia (Limonia) sciophila (Osten Sacken, 1877).—Arizona Creek, 6,790 ft., July 3, 1941; Jenny Lake, 6,780 ft., July 3, 1941; Leigh Lake, Station 5, 6,870 ft., July 10-12, 1941.

Limonia (Limonia) solitaria (Osten Sacken, 1859).—Moran bog, 6,800 ft., July 5, 1941; Jenny Lake, 6,780 ft., July 1-3, 1941; Leigh Lake, 6,870 ft., July 10-12, 1941.

Limonia (Discobola) annulata (Linnaeus, 1758) (*argus* Say, 1824).—Moran, 6,800 ft., August 23, 1941 (J. L. & G. H. Sperry).

Limonia (Dicranomyia) athabasca (Alexander, 1927).—Moran bog, Station 2, 6,800 ft., July 2-5, 1941; bog near Jackson Lake, 6,770 ft., July 15, 1941.

Limonia (Dicranomyia) brevivena (Osten Sacken, 1869).—Moran bog, 6,800 ft., July 3, 1941; Jackson Lake, 6,780 ft., July 2, 1941.

Limonia (Dicranomyia) citrina (Doane, 1900).—Along Cascade Trail, Grand Tetons, between 6,900 and 8,800 ft., July 4-9, 1941; again on July 8, 1942; especially numerous on wet rocks (Station 3) below Hidden Falls; at these lower altitudes on July 4th, only females were found but males were still flying at the higher levels.

Limonia (Dicranomyia) halterata (Osten Sacken, 1869).—Arizona Creek, 6,790 ft., July 1, 1941.

Limonia (Dicranomyia) humidicola dampfi (Alexander, 1925).—Jenny Lake, July 3, 1941; Leigh Lake, July 10-12, 1941; both discussed under Station 5. This is the same form as reported from the Yellowstone as being *humidicola* (Osten Sacken, 1859); it now appears that the Rocky Mountain materials actually pertain to the subspecies listed above.

Limonia (Dicranomyia) longipennis (Schummel, 1829) (*immemor* Osten Sacken, 1861).—Moran, bog, 6,800 ft., July 2, 1941; along Buffalo Creek, near Moran, July 9, 1942.

Limonia (Dicranomyia) morioides (Osten Sacken, 1860).—Arizona

Creek, 6,790 ft., July 1-8, 1941; Moran bog, 6,800 ft., July 5, 1941; Buffalo Creek, near Moran, July 9, 1942; Death Canyon, 7,800 ft., July 14, 1941.

Limonia (Dicranomyia) penicillata (Alexander, 1927).—Moran bog, 6,800 ft., July 5, 1941; Buffalo Creek, near Moran, July 9, 1942; Twogwotee Pass, 9,650 ft., September 13, 1941 (Knowlton & Thornley).

Limonia (Dicranomyia) venusta (Bergroth, 1888) (negligens Alexander, 1927).—Moran, August 24, 1941 (J. L. & G. H. Sperry); Jenny Lake, 6,790 ft., August 5, 1942 (Sperry); Leigh Lake, 6,870 ft., July 10-12, 1941; Hidden Falls, Station 3, 6,900 ft., July 8, 1942; a few of the individuals were still teneral.

Antocha (Antocha) monticola Alexander, 1917.—Along the banks of the Snake R., Moose, Wyoming, July 6, 1942.

Elliptera astigmatica Alexander, 1912.—On wet rocky outcrops below Hidden Falls, Station 3, July 4, 1941; July 8, 1942; resting and crawling about among patches of *Saxifraga* and *Lewisia*.

Dicranoptycha quadrivittata Alexander, 1919.—Arizona Creek, 6,790 ft., July 8, 1941 (W. H. Harrison); along Pilgrim Creek, 6,800 ft., July 5, 1942; July 25, 1942 (J. L. & G. H. Sperry); along the Snake R., Moose, Wyoming, 6,800 ft., July 6, 1942; among rich riverside vegetation.

PEDICIINI

Pedicia (Tricyphona) degenerata (Alexander, 1917).—Jenny Lake, Station 5, 6,780 ft., July 4, 1941; Leigh Lake, 6,870 ft., July 12, 1941, very common; Death Canyon, 7,000 ft., July 14, 1941; one male from the last-named station has the wings even more reduced in size than usual but still with the venation clearly defined though distorted (σ^7 . Length, about 6 mm.; wing, 4 x .38 mm.).

Pedicia (Tricyphona) sparsipuncta (Alexander, 1920).—Jenny Lake, 6,780 ft., July 3, 1941.

Ornithodes harrimani Coquillett, 1900.—Hidden Falls, Station 3, 6,900 ft., July 8, 1942, resting on the face of perpendicular wet rocks (M. M. Alexander); Twogwotee Pass, Station 6, 9,650 ft., July 9, 1942; swept from dense willow patches.

Dicranota (Dicranota) montana Alexander, 1920.—Arizona Creek, 6,790 ft., July 4, 1942 (M. M. Alexander); flying close to stream margin.

Dicranota (Dicranota) tetonicola sp. nov.—General coloration dark gray, the praescutum with three blackish stripes; antennae short, 13-segmented; knobs of halteres dark brown; legs black, the femoral bases restrictedly brightened; wings with a strong blackish tinge, stigma oval, still darker; cell R_3 sessile or virtually so, R_{2+3+4} usually lacking or reduced to a punctiform element; cell M_1 present; male hypopygium with the lateral tergal arms very

small, slender-stemmed, terminating in a small head; apex of basistyle produced into a stout dorsal lobe; interbase a strong powerful rod, at apex expanded into an oval blade that terminates in a small apiculate point.

♂. Length, about 6.5 mm.; wing, 8 mm.; antenna, about 1-1.1 mm.

Rostrum black, sparsely pruinose; palpi black. Antennae short black throughout, 13-segmented; first flagellar segment cylindrical, nearly twice as long as second; succeeding segments oval, with the lower face a little produced; terminal segment reduced, about one-third as long as the penultimate; longest verticils a little shorter than the segments; besides the verticils, an abundant vestiture of short erect dark setulae. Head dark brownish gray; anterior vertex broad; vertical tubercle low.

Pronotum dark gray. Mesonotum dark gray, the praescutum with three blackish stripes, the median one vaguely divided by a paler vitta; scutal lobes variegated by blackened areas. Pleura and pleurotergite gray, the ventral sternopleurite darker; dorsopleural membrane infuscated. Halteres relatively long, stem pale, knob dark brown. Legs with the coxae gray; trochanters testaceous; remainder of legs black, the femoral bases restrictedly brightened. Wings (Fig. 20) with a strong blackish tinge; costal border and a seam along vein *Cu* still darker; stigma oval, even darker brown; veins dark brown. Venation: *Sc*₁ ending opposite the supernumerary crossvein in cell *R*₁, *Sc*₂ a

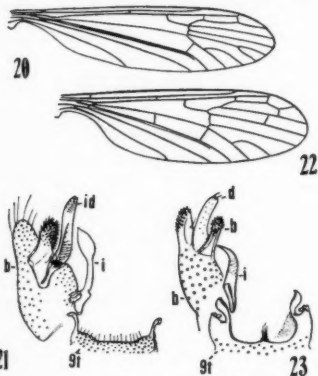


Fig. 20. *Dicranota (Dicranota) tetonicola* sp. nov.; venation.

Fig. 21. *Dicranota (Dicranota) tetonicola* sp. nov.; male hypopygium.

Fig. 22. *Dicranota (Polyangaeus) megaloops* sp. nov.; venation.

Fig. 23. *Dicranota (Polyangaeus) megaloops* sp. nov.; male hypopygium.

(Symbols: *b*, basistyle; *d*, dististyle; *i*, interbase; *id*, inner dististyle; *t*, tergite.)

distance before the origin of *R*₃ greater than the length of the latter; vein *R*₂ erect; cell *R*₃ sessile or with *R*₂₊₃₊₄ indicated by a punctiform element; cell *M*₁ present; *m-cu* about its own length beyond the fork of *M*.

Abdomen black, sparsely pruinose, the pleural membrane conspicuously pale; hypopygium large, black. Male hypopygium (Fig. 21) with the tergite, *9t*, broad, concave across the margin, the lateral angles produced, terminating in a very small, slender-stemmed arm with an expanded or capitate head. Basistyle, *b*, with the apical lobe large and stout, with long coarse pale setae; interbase, *i*, a strong powerful rod, at apex expanded into an oval blade that terminates in a small apiculate point. Outer dististyle, *od*, broad, the distal

half with abundant blackened spinous setae. Inner dististyle, *id*, a flattened elongate blade, its tip narrowly obtuse.

Holotype, ♂, Jenny Lake, Station 5, 6,790 ft., July 6, 1941 (*C. P. Alexander*). *Paratopotype*, 1 ♂. The types were captured by sweeping vegetation along banks of Cascade Creek close to the lake margin.

Dicranota (Dicranota) tetonicola is entirely distinct from all other Nearctic species described to this date. It is well distinguished by the blackened wings, with distinctive venation, and by the structure of the male hypopygium, especially the produced basistyle and the shapes of the interbase and lateral arms of tergite.

Dicranota (Plectromyia) reducta (Alexander, 1921).—Leigh Lake, Station 5, 6,870 ft., July 10-12, 1941, abundant; Indian Paintbrush Canyon, 7,500 ft., July 13, 1941.

Dicranota (Polyangaeus) megalops sp. nov.—Fully-winged in both sexes; general coloration dark brown or brownish black the praescutal stripes poorly differentiated; antennae with flagellar segments tending to fuse into groups of two or three, more especially the proximal ones; eyes (male) large and protuberant; halteres pale; tibiae white with both ends narrowly darkened; male hypopygium with the median tergal lobe very narrow, tipped with about four large setae.

♂. Length, about 4.5 mm.; wing, 4.2-5.2 mm.; antenna, about 0.7-0.9 mm.

♀. Length, about 4.4-5 mm.; wing, about 4.5-5 mm.

Rostrum and palpi black. Antennae with scape and pedicel brownish black, flagellum yellowish brown to dark brown; antennal segments varying in number from 12 to 14 segments; basal flagellar segments tending to become united into one or more paired segments, or into a more extensive fusion, in some cases involving the proximal three flagellar segments; in some cases, the outermost pair of segments likewise more or less fused; unfused segments short-oval to oval. Head dark brownish gray; eyes of male very large and protuberant, broadly contiguous beneath but widely separated by the vertex; anterior vertex about three times the diameter of scape.

Pronotum restricted in size, testaceous brown. Mesonotum almost uniform dark brown or brownish black, the three praescutal stripes poorly differentiated. Pleura brownish black; dorsopleural membrane pale. Halteres pale. Legs with the coxae testaceous, the fore pair a little paler than the others; trochanters yellow; femora brownish yellow, the tips narrowly blackened; tibiae white, with both base and apex narrowly blackened; proximal tarsal segments pale brown, the outer segments darker. Wings (Fig. 22) broad, subhyaline, with restricted dark clouds, as follows: Over supernumerary crossvein in cell *Sc*; origin of *R*₅; cord; *R*₂ over all outer supernumerary crossveins; veins pale brown, darker in the clouded portions. Wings equally developed in both sexes. Venation: Supernumerary crossveins in cells *R*₃, *R*₄ and *M*, additional to the usual one in cell *R*₁; venation unusually variable, especially as regards cell

M_1 which, while normally present, may be lacking (as figured) or in process of loss by atrophy of vein M_2 .

Abdomen, including hypopygium, brownish black. Male hypopygium (Fig. 23) with the median region of tergite, 9t, produced into a slender lobe that bears about four elongate setae at and near summit; lateral tergal arms appearing as conspicuous flattened blades, narrowest at base, expanded at apex into a semicircular head; still laterad of the insertion of the blade with two smaller lobes on the incurved margin of the tergite. Basistyle, b , with two slightly unequal apical lobes, the outer one stouter than the inner, both with abundant short blackened spines; interbase, i , a strong powerful blade, very broad at base, at about three-fourths the length bent almost at a right angle and thence narrowed to a long straight point; surface of interbase before the bend with abundant microscopic setulae. Dististyle, d , in the notch formed by the lobes of the basistyle, appearing as a slender yellow blade, broadest at base, narrowed very gradually to the obtuse tip which bears two strong spinous setae; elsewhere on surface the setae sparse and reduced in size.

Holotype, ♂, Moran bog, Station 2, 6,800 ft., July 2, 1941 (*C. P. Alexander*). *Allotopotype*, ♀, pinned with type. *Paratopotypes*, 1 ♂, pinned with type; numerous additional ♂♂ and a few ♀♀, July 2-5, 1941 (*C. P. & M. M. Alexander*).

Dicranota (Polyangaeus) megalops is readily told from the only other discovered Rocky Mountain species, *D. (P.) subapterogyne* (Alexander, 1943) by the large eyes of the males and the fully-winged females. From the still more western, *D. (P.) maculata* (Doane, 1900), it is told by the unusually large size of the head, especially across the eyes, and in the details of coloration, as the almost uniform dark tone of the body. From a recent survey of the greatly developed *Dicranota* fauna of Asia, particularly the Himalayan region, it seems best to place various groups, including *Polyangaeus* Doane, 1900, as subgenera rather than to attempt to maintain them as full genera.

The present fly was found in a very restricted area in the Moran bog. Here they were found resting on herbs beneath the willow thickets and a series of more than fifty specimens was taken. Toward evening the males appeared in small swarms of from six to eight individuals, dancing close to the ground alongside the willow thickets.

Dicranota (Polyangaeus) subapterogyne (Alexander, 1943).—Jenny Lake, 6,780 ft., July 4, 1941; Hidden Falls, 6,900 ft., 6,900-7,000 ft., July 3-8, 1941; Leigh Lake, 6,875 ft., July 10, 1941; Moran, bog, 6,800 ft., July 2, 1941; all part of type series. For an account of the habits and occurrence of this fly, with its nearly wingless females, the preceding part of this series should be consulted (Alexander, 1943: 743).

Dicranota (Raphidolabis) cayuga (Alexander, 1916).—Jenny Lake, 6,780 ft., July 6, 1941; Cascade Trail, above Station 4, 8,800 ft., July 9, 1941.

Dicranota (Raphidolabis) subseasilis (Alexander, 1921).—Jenny Lake,

Station 5, 6,780 ft., July 3-6, 1941; Leigh Lake, Station 5, 6,870 ft., July 10-12, 1941.

Ula (Ula) paupera Osten Sacken, 1869.—Arizona Creek, 6,790 ft., July 5, 1942, beneath evergreens; Leigh Lake, 6,870 ft., July 10, 1941.

HEXATOMINI

Austrolimnophila badia (Doane, 1900).—Jenny Lake, 6,780 ft., July 3-5, 1941; Hidden Falls, 6,900 ft., July 8, 1942.

Archilimnophila subunica (Alexander, 1920).—Hidden Falls, 6,900 ft., July 3, 1941; male, with both wings badly deformed.

Phyllolabis lagganensis Alexander, 1931.—Below Hidden Falls, Station 3, on wet rocky exposures, July 4, 1941.

Limnophila (*Elaeophila*) *aleator* sp. nov.—General coloration gray, the praescutum with four entire dark brown stripes; antennae brownish black, relatively short; knobs of halteres dark brown; femora obscure yellow, the tips narrowly darkened; remainder of legs medium brown; wings relatively narrow, spotted and dotted with brown, including six larger costal areas; cells of posterior three-fourths of wing with relatively numerous brown dots; male hypopygium with the outer dististyle relatively broad, its outer flange broadly attached.

♂. Length, about 6.5-7 mm.; wing, 8 x 1.8-8.5 x 1.9 mm.; antenna, about 1.3-1.4 mm.

♀. Length, about 7-8 mm.; wing, 8-9 mm.

Rostrum brown, sparsely pruinose; palpi black. Antennae relatively short, brownish black, the scape sparsely pruinose; basal flagellar segments short-oval, the outer ones more elongate, with conspicuous verticils. Head dark gray, the broad anterior vertex with a narrow blackish spot or short stripe.

Pronotum brownish gray, with a darker brown median line. Mesonotal praescutum with the ground yellowish gray, with four entire, dark brown stripes; pseudosutural foveae large and black; scutum brownish gray, each lobe and the central region patterned with brown; posterior sclerites of notum dark brown, sparsely pruinose. Pleura dark brown, heavily gray pruinose; dorso-pleural membrane darkened. Halteres yellow, the knobs dark brown. Legs with the coxae obscure testaceous yellow, the fore and middle pairs narrowly more darkened basally; trochanters obscure brownish yellow; femora obscure yellow, the tips narrowly darkened; remaining segments of legs medium brown. Wings (Fig. 24) relatively narrow, as shown by the measurements; ground color yellow, more saturated in the prearcular and costal regions; a series of six major brown costal spots, all reaching the anterior margin, the first more broken, at *h* and above the arculus; third area at origin of *Rs*, fourth at fork of *Sc*, fifth area stigmal, the sixth at the end of vein *R*₃; more restricted brown clouds at cord, outer end of cell 1st *M*₂, over the supernumerary crossvein, and at end of vein 2nd *A*; relatively numerous, small, paler brown dots in the cells of posterior three-fourths of wing, lacking or virtually so along the

brightened costal border; veins brown, yellow in the costal interspaces. Venation: R_s long, angulated and sometimes spurred at origin; R_{2+3+4} relatively long, subequal to or slightly longer than cell 1st M_2 , virtually in longitudinal alignment with R_s ; R_2 subequal to or longer than R_{2+3} ; cell 1st M_2 relatively small, $m-cu$ at or before midlength.

Abdominal segments obscure brownish yellow or light brown, the lateral and posterior borders of the segments darker brown; sternites with the ground somewhat clearer yellow; a narrow darker subterminal ring; hypopygium medium brown. Male hypopygium (Fig. 27) with the basistyle, b , relatively stout, without elongate setae as in *angustior*. Outer dististyle, od , broader than in *superlineata*, the outer flange broadly attached, relatively small and

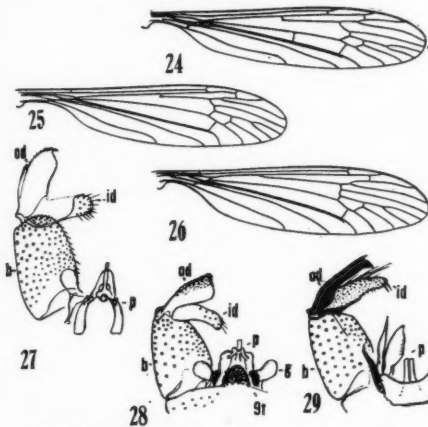


Fig. 24. *Limnophila (Elacophila) aleator* sp. nov.; venation.

Fig. 25. *Limnophila bigladii* sp. nov.; venation.

Fig. 26. *Limnophila tetonicola* sp. nov.; venation.

Fig. 27. *Limnophila (Elacophila) aleator* sp. nov.; male hypopygium.

Fig. 28. *Limnophila (Elacophila) shannoni* Alexander; male hypopygium.

Fig. 29. *Limnophila tetricola* sp. nov.; male hypopygium.

(Symbols: b , basistyle; g , gonapophysis; id , inner dististyle; od , outer dististyle; p , phallosome; t , tergite.)

inconspicuous. Inner dististyle, id , with only the distal third sclerotized and provided with setae, the basal portion, excepting a narrow band along the lower or cephalic border, consisting of white membrane. Phallosome, p , with the gonapophyses appearing as relatively large and conspicuous oval blades, much larger than in *superlineata*; phallosomic plate narrowed outwardly, not forming, square shoulders, as in *superlineata*.

Holotype, ♂, Arizona Creek, Station 1, 6,790 ft., July 2, 1941 (*C. P. Alexander*). *Allotopotype*, ♀, July 8, 1941. *Paratopotypes*, 6 ♂ ♀, 6,790-6,800 ft., July 1-8, 1941 (*C. P. & M. M. Alexander*); *paratypes*, a few ♂ ♀, 5 miles south of Glendale, Utah, along stream seepage, May 5, 1943 (*G. F. Knowlton*).

The only generally similar regional species is *Limnophila (Elacophila) superlineata* Doane, 1900, which is well-distinguished by the broad wings, with a different arrangement of pattern, and in the details of structure of the male hypopygium, as discussed above.

Limnophila (Elaeophila) angustior Alexander, 1919.—Arizona Creek, 6,790 ft., July 4-8, 1941.

Limnophila (Elaeophila) shannoni Alexander, 1921.—The types were from Moscow Mt., Idaho, collected July 25, 1920, by R. C. Shannon. I have not seen any additional specimens until the present material.

Leigh Lake, Station 5, 6,870 ft., July 10-12, 1941. I am transferring both this species and *L. (E.) bifida* Alexander, 1921, from the subgenus *Idioptera* Macquart, 1834, where they were originally assigned, to *Elaeophila* Rondani, 1856. Such a treatment conforms to that of the late Dr. Fred W. Edwards (Trans. Soc. British Ent., 5, pt. 1:76-84; 1938) where, by a readjustment of characters, the various British species previously referred to *Idioptera* on the basis of length of the antennae in the male sex were placed in *Elaeophila* on other characters of venation and hypopygial structure. Both of the Nearctic species above mentioned have the male antennae elongate and in this respect differ widely from the remaining rather numerous species of *Elaeophila*, being evidently more nearly allied to the northern European *L. (E.) trimaculata* (Zetterstedt, 1838).

Male hypopygium (Fig. 28) with the median region of tergite, 9t, produced caudad into a rounded or oval lobe that is densely clothed with setae. Outer distyle, *od*, simple, appearing as a blackened blade, expanded outwardly, its apex truncated; outer apical portion with microscopic blackened spinulae, the extreme angle more or less produced. Inner dististyle, *id*, subequal in length to the outer style, gradually narrowed to the obtuse tip. Gonapophyses, *g*, appearing as oval plates, the apex smooth and evenly rounded, the inner or caudal margin more roughened. Phallosome and aedeagus short.

Limnophila (Phylidorea) adusta Osten Sacken, 1859.—String Lake, bog, 6,870 ft., July 7, 1941. The first record of this eastern North American species from the west; hitherto not known from west of Wisconsin and Illinois.

Limnophila (Phylidorea) claggi Alexander, 1930.—Moose Ponds, near Jenny Lake, 6,700 ft., July 6, 1941; Jenny Lake, 6,790 ft., July 3, 1941; Leigh Lake, Station 5, 6,870 ft., July 10-12, 1941; Cascade Trail, in Engelmann Spruce forest, 8,000 ft., July 9, 1941.

Limnophila (Phylidorea) platyphallus Alexander, 1926.—Moran bog, 6,800 ft., July 2-5, 1941.

Limnophila (Phylidorea) tepida Alexander, 1926.—Moran bog, 6,800 ft., July 2-5, 1941; Cascade Trail, in boggy areas in the Engelmann Spruce forest, 8,000-8,200 ft., July 3-9, 1941. Closely allied to *L. (P.) flavipila* Doane, 1900.

Limnophila bigladia sp. nov.—Allied to *mcdunnoughi*; general coloration dark gray, the praescutum with four brown stripes; fore femora extensively blackened; wings cream-colored, with a restricted but conspicuous brown pattern; outer radial field darkened; area near base of cell *R* very reduced; cell 1st *M*₂ rectangular; abdominal sternites yellow; subterminal seg-

ments blackened; male hypopygium with the outer dististyle broadly flattened; gonapophyses appearing as relatively small, slender, divergent blades that exceed the aedeagus in length.

♂. Length, about 11-12 mm.; wing, 10-11.5 mm.; antenna, about 1.6-1.7 mm.

♀. Length, about 13 mm.; wing, 12 mm.

Rostrum black, pruinose; palpi brown, passing into black. Antennae with scape and pedicel black; flagellum dark brown, the outer segments even darker; basal flagellar segments subglobular, relatively large and crowded, with verticils on their dorsal surface only; on about the sixth and succeeding segments with verticils on both faces, very long and conspicuous, the segments elongate. Head gray, the setigerous punctures brown; head only moderately narrowed behind; anterior vertex about three times as wide as the diameter of scape.

Pronotum relatively small, gray. Mesonotum dark gray, the praescutum with four brown stripes, the humeral region lighter gray, enclosing the large, conspicuous, black pseudosutural foveae; scutal lobes with weakly darkened centers; posterior sclerites of notum light gray. Pleura gray, the dorsopleural region only slightly brightened. Halteres uniformly pale yellow. Legs with fore and middle coxae dark gray, brightened at apices, posterior coxae more extensively pale; trochanters reddish; fore femora in types extensively blackened, as in *nigrofemorata*, with about the proximal third yellow; middle and hind femora usually with the tips more narrowly blackened, especially the middle pair; in other specimens, all femora equally and broadly blackened; tibiae brown, the tips narrowly blackened; tarsi black. Wings (Fig. 25) with the ground color creamy, the prearcular and costal fields clearer yellow; a restricted but conspicuous brown pattern, including the stigma and a complete band at cord; outer end of cell 1st M_2 ; wing-tip, especially in outer radial field; a large circular spot at origin of R_s ; a small cloud near outer end of cell 1st A adjoining the vein; a small to scarcely indicated darkening in cell R adjoining the vein, about mid-distance between arculus and origin of R_s , this much smaller than in *nigrofemorata*. Venation: R_s square and spurred at origin; R_{2+3+4} relatively short, up to about one-half longer than the basal section of R_5 ; cell 1st M_2 rectangular, longer than in related species.

Abdomen yellow; basal tergite and proximal ring of second darkened; succeeding tergites brown with the basal lateral portions yellow; on the fifth and succeeding tergites more uniformly brown; sternites clear yellow, the intermediate segments with a weak dark area on posterior border; eighth and ninth segments black; styli paler. Male hypopygium with the dorsal lobe of basistyle much produced. Outer dististyle of about the same shape as in *mcduwoughi*, broadest across the proximal half, the greatest width at about two-thirds the length; apex unequally bidentate. Gonapophyses appearing as relatively small, slender, divergent blades that exceed the aedeagus in length.

Holotype, ♂, Death Canyon, Grand Tetons, 7,800 ft., July 14, 1941 (C. P. Alexander). *Allotopotype*, ♀, with the type. *Paratopotypes*, 25 ♂ ♀; *paratypes*, 1 ♀, Arizona Creek, Station 1, 6,790 ft., July 1, 1941 (C. P. Alexander); 1 ♂, Mount Rainier, Washington, 2,900 ft., July 28, 1940 (H. &

M. Townes); 1 ♂, 1 ♀, Banff, Alberta, July 18-25, 1922 (C. B. D. Garrett); other material in this series in the Canadian National Collection (as *mcduunnoughi*).

Although closely allied to *Limnophila mcduunnoughi* Alexander, 1926, and *L. nigrofemorata* Alexander, 1927, the present fly is distinguished by various characters, particularly in the structure of the male hypopygium. From *mcduunnoughi* it differs in the venation and pattern of the wings and legs, and, especially, in the conformation of the gonapophyses, which in *mcduunnoughi* are unusually large and flattened, much more complex in structure. From *nigrofemorata*, it differs in the structure of the hypopygium, particularly the outer dististyle and the gonopophyses (see figure, Proc. U. S. Nat. Mus., 72, art. 2, pl. 1, fig. 7; 1927; outer dististyle). In their general appearance all three species much resemble large, showy species of the subgenus *Phylidorea* but form a distinct and isolated group of forms that it seems better not to attempt to assign to any particular subgeneric group at the present time.

The main series of types was swept from low grasses and rushes near the banks of Death Creek, near the Forks. The males were flying very close to the ground and were much in evidence.

Limnophila occidens Alexander, 1924.—Leigh Lake, Station 5, 6,870 ft., July 10-12, 1941; Indian Paintbrush Canyon, 8,000 ft., July 13, 1941; Cascade Trail, 8,000 ft., in Engelmann spruce association, July 3, 1941.

Limnophila tetonicola sp. nov.—Size large (wing, male, 10 mm. or more); general coloration of notum brownish gray, the posterior sclerites and the pleura clearer gray; antennae relatively short, the proximal three flagellar segments enlarged, the outer ones very slender, with conspicuous verticils; wings brownish yellow, the oval stigma dark brown; *Rs* very long, subequal to the distal section of *R*₅; cell *M*₁ longer than its petiole; *m-cu* at or beyond midlength of cell 1st *M*₂; abdomen brownish black, the basal sternites with their central portion obscure yellow; male hypopygium with the outer dististyle a nearly straight rod, with a suberect spine before the decurved apex.

♂. Length, about 9.5-11.5 mm.; wing, 10.5-13.5 mm.; antenna, about 1.9-2.1 mm.

Rostrum black, brownish gray pruinose; palpi black. Antennae relatively short; scape brownish black above, lighter brown beneath; pedicel and flagellum black; pedicel large, pyriform; basal three flagellar segments large, especially the first, outwardly becoming progressively smaller, subcylindrical or with the lower face slightly produced; succeeding segments passing into long-cylindrical, with long conspicuous verticils, the longest exceeding the segments in length; terminal segment a little longer than the penultimate. Head brownish gray; anterior vertex relatively wide, about three times the diameter of scape; head only moderately narrowed behind.

Pronotum moderately massive; scutum brownish gray; scutellum brightened, obscure yellow medially, infuscated on sides. Mesonotum almost uniform dark brown, the praescutum without clearly differentiated stripes, the interspaces about concolorous with the stripes, the central region before suture more

reddened; pseudosutural foveae lying close to lateral border, pale in color and very inconspicuous; surface of notum sparsely pruinose, the lateral and humeral regions of praescutum more yellowish gray; scutellum and postnotum clearer gray pruinose. Pleura gray pruinose; dorsopleural membrane yellow. Halteres with stem yellow, clearer at base, knob infuscated. Legs with coxae infuscated, pruinose, paler at tips, the posterior pair somewhat more uniformly pale; trochanters obscure yellow; femora obscure yellow, more brownish yellow outwardly, the tips narrowly and inconspicuously darker brown; tibiae and basitarsi light brown, the tips narrowly blackened; remainder of tarsi black; claws long and simple. Wings (Fig. 26) large, with a strong and almost uniform brownish yellow suffusion; prearcular and costal fields slightly more yellowish; stigma oval, dark brown, relatively conspicuous; certain of the veins, especially in the radial field, very insensibly bordered by darker; veins brown, more brownish yellow in the brightened fields. Venation: Sc relatively long. Sc_1 ending opposite fork of R_{2+3+4} ; Sc_2 at its tip; R_s very long, subequal to or a little longer than the distal section of R_5 ; R_{2+3+4} relatively short, varying from subequal to less than twice the basal section of R_5 or nearly subequal to R_{1+2} ; cell M_1 longer than its petiole; $m-cu$ at or beyond midlength of cell 1st M_2 ; anterior arculus present.

Abdomen brownish black; basal sternites obscure yellow on median portion, the sides blackened, this pale color narrowed on outer segments; subterminal segments uniformly dark; hypopygium brightened, obscure brownish yellow to dark brown. Male hypopygium (Fig. 29) with the basistyle, b , stout, simple, not produced at apex nor with an interbasal process. Outer dististyle, od , a nearly straight blackened rod, the apex slightly decurved into a strong spine, with a nearly equal suberect spine on outer margin a short distance back from tip. Inner dististyle, id , stout, narrowed to the obtuse tip, terminating in two strong setae, with four or five longer and more slender bristles on outer margin; remaining surface of style with abundant smaller setae and setulae. Phallosome, p , with the apophyses longer than the aedeagus.

Holotype, ♂, Indian Paintbrush Canyon, Grand Tetons, 8,000 ft., July 13, 1941 (*C. P. Alexander*). *Paratopotypes*, 11 ♂♂, 7,800-8,000 ft., July 13, 1941; 1 ♂, Leigh Lake, Station 5, 6,870 ft., July 10, 1941 (*C. P. Alexander*); 1 ♂, Indian Paintbrush Canyon, 9,000 ft., August 7, 1942 (*J. L. Sperry*).

As with the preceding species, I am quite uncertain as to the strict subgeneric position of the present fly. It may possibly be referred to *Phylidorea* but the great length of R_s would seem to preclude such an assignment. The fly needs no comparison with any of the species so far made known. The main series of types was swept from a marshy area along the stream in Indian Paintbrush Canyon. They would swarm in groups of two or three individuals very close to the ground beneath the alpine firs.

Pilaria imbecilla (Osten Sacken, 1859).—In a nearly dessicated wet area where *Pedicularis groenlandica* Retz., was the dominant plant, near Jackson Lake, 6,770 ft., July 15, 1941.

Pilaria osborni (Alexander, 1914).—Associated with the last named. The

fly is very close to the Palearctic *meridiana* Staeger, 1840, and may prove to be identical, in which case it would have a vast subpolar range throughout the North Temperate zone.

Hexatoma (Eriocera) eriophora (Williston, 1893).—Pilgrim Creek, near Moran, 6,800 ft., July 5, 1942.

Hexatoma (Eriocera) velveta (Doane, 1900).—Arizona Creek, Station 1, along stream border, 6,790 ft., July 8, 1941.

ERIOPTERINI

Gonomyia (Idiocera) shannoni Alexander, 1926.—Jenny Lake, 6,790 ft., July 4, 1941; swarming in small groups beneath the Engelmann spruce in relatively dry places along the trail. The habitat is quite different from that frequented by *G. (I.) proserpina* Alexander, 1943, in the Yellowstone (Alexander, 1943: 749).

Gonomyia (Gonomyia) aciculifera Alexander, 1919.—Arizona Creek, Station 1, 6,790 ft., July 1-8, 1941, very abundant on herbage near stream.

Gonomyia (Gonomyia) bihamata Alexander, 1943.—Hidden Falls, 6,900 ft., July 4, 1941; Jenny Lake, 6,790 ft., July 6, 1941; Leigh Lake, 6,870 ft., July 10, 1941.

Gonomyia (Gonomyia) extensivena Alexander, 1943.—Cascade Canyon, Station 4, 8,200 ft., July 9, 1941.

Gonomyia (Gonomyia) vafra sp. nov.—Allied to *extensivena*; general coloration of mesonotum brownish gray, the posterior border of scutellum yellow; antennae black throughout; fore coxae blackened; wings with a grayish tinge, the prearcular and costal fields more yellowed; Sc relatively short, Sc_1 ending about opposite origin of R_s , Sc_2 a short distance from its tip; R_{2+3+4} only slightly arcuated; cell $1st\ M_2$ only gently widened outwardly; abdominal tergites dark brown, sternites and hypopygium yellow; male hypopygium with the outer dististyle of moderate length, with a long dark-colored lateral flange; inner dististyle with a single simple blackened spine.

♂. Length, about 4.5 mm.; wing, 5-5.2 mm.

Rostrum yellow; palpi black. Antennae black throughout, relatively elongate; flagellar segments long-oval, passing into elongate. Head dark gray, indistinctly patterned with reddish on vertex.

Mesonotal praescutum light yellow with three brownish gray stripes that are only vaguely separated; scutal lobes similarly darkened, the median region pale; scutellum darkened medially at base, the posterior border obscure yellow; mediotergite brownish gray, the lateral borders yellow; pleurotergite entirely yellow. Pleura yellow, the propleura and mesepisternum patterned with dark brown or brownish black, including the extensive propleural area and less evident darkenings on the ventral anepisternum and ventral sternopleurite. Halteres brownish black, the base of stem pale. Legs with fore coxae brown-

ish black, the remaining coxae testaceous yellow; trochanters yellow; femora, tibiae and basitarsi brownish yellow, somewhat darker at their tips; remainder of tarsi black. Wings (Fig. 30) with a grayish tinge, the prearcular and costal fields more yellowed; stigma pale brown, ill-delimited and poorly indicated against the ground; veins brown. Venation: Sc relatively short, Sc_1 ending opposite the origin of R_s , Sc_2 a distance before this origin that is subequal to m ; R_{2+3+4} only slightly arcuated; cell $1st\ M_2$ rectangular, only slightly arcuated; cell $1st\ M_2$ rectangular, only slightly widened outwardly, subequal in length to vein M_4 beyond it; $m-cu$ about one-fifth to one-sixth its length beyond the fork of M .

Abdominal tergites dark brown, the incisures of the outer segments paler; sternites and hypopygium yellow. Male hypopygium (Fig. 36) with the outer dististyle, od , shorter than in *extensivena*, its darkened flange longer. Inner dististyle, id , with a single simple blackened spine. Gonapophyses unequal. Apex of aedeagus shaped as in the group, the subterminal lobes obtuse, the tips nearly hyaline.

Holotype, ♂, Arizona Creek, Station 1, 6,790 ft., July 4, 1942 (C. P. Alexander). *Paratopotype*, ♂.

Although in its general appearance, *Gonomyia* (*Gonomyia*) *vafra* is rather different from *G. (G.) extensivena* Alexander, there can be no question of the close relationships between the two flies. The hypopygial differences have been discussed above. In *extensivena*, the wings are broader, with the individual cells correspondingly wider, and with vein Sc extending to a varying distance beyond the origin of R_s .

Rhabdomastix (*Sacandaga*) *leonardi* Alexander, 1930.—Arizona Creek, 6,790 ft., July 1-8, 1941, July 5, 1942; abundant on low willows along the stream.

Rhabdomastix (*Sacandaga*) *neolurida* Alexander, 1943.—The type material was from Arizona Creek, 6,700-6,790 ft., July 8, 1941. Additional specimens from the same station July 5, 1942.

Rhabdomastix (*Sacandaga*) *subcaudata* Alexander, 1927.—Cascade Trail, Grand Tetons, below Lake Solitude, 8,800 ft., July 9, 1941.

Erioptera (*Empeda*) *tristimonia* Alexander, 1943.—Jenny Lake, Station 5, 6,780 ft., July 6, 1941.

Erioptera (*Erioptera*) *septemtrionis* Osten Sacken, 1859.—Leigh Lake, 6,870 ft., July 10-12, 1941; Death Canyon, 7,000 ft., July 14, 1941 (*M. M. Alexander*).

Erioptera (*Mesocyphona*) *distincta* Alexander, 1912.—Arizona Creek, Station 1, 6,790 ft., July 1, 1941.

Erioptera (*Symplecta*) *cana* (Walker, 1848).—Arizona Creek, 6,790 ft., July 2, 1941; Moran bog, 6,800 ft., July 5, 1941; Leigh Lake, 6,870 ft., July 10-12, 1941; Pilgrim Creek, near Moran, 6,800 ft., July 5, 1942.

Erioptera (Psiloconopa) aperta (Coquillett, 1905) (*mormon* Alexander, 1927).—Cascade Creek, below Hidden Falls, 6,850 ft., July 4-6, 1941, close to the stream margin; Death Canyon, 7,800 ft., July 14, 1941.

Erioptera (Psiloconopa) gaspicola (Alexander, 1929).—Arizona Creek, Station 1, 6,790 ft., July 1-8, 1941.

Erioptera (Psiloconopa) shoshone sp. nov.—Belongs to the *meigenii* group; size small (wing, under 4 mm.); general coloration black, the surface more or less opaque; pronotum, mesonotal scutellum and pleura variegated with yellow; palpi, antennae and legs uniform black; halteres clear yellow; wings subhyaline; cell M_2 open by the atrophy of m ; $m-cu$ a short distance before fork of M ; vein 2nd A evenly convex; abdomen black, the outer segments ringed caudally with yellow; male hypopygium with both dististyles small and simple, the glabrous outer style blackened on distal portion; both sets of gonapophyses appearing as simple slender rods with acute tips.

♂. Length, about 2.8-3 mm.; wing, 3.2-3.5 mm.; antenna, about 0.5 mm.

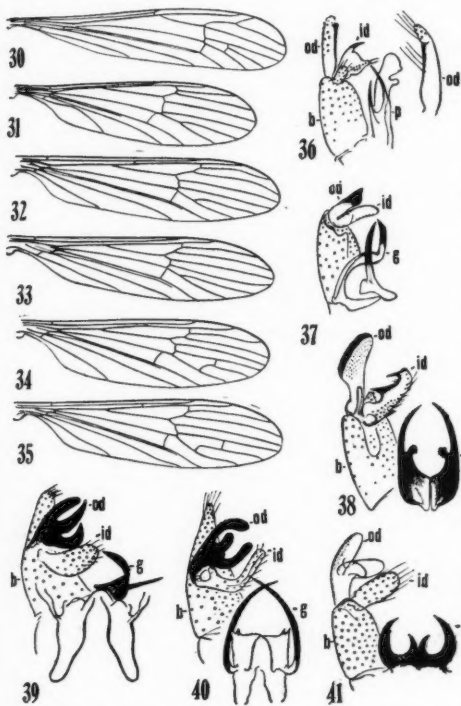
♀. Length, about 3-3.2 mm.; wing, 3-3.5 mm.

Rostrum and palpi black. Antennae black throughout; flagellar segments oval, with verticils of moderate length. Head brownish gray; anterior vertex relatively narrow; eyes of male large.

Pronotum light yellow, variegated on central portion with brown. Mesonotum black, the surface slightly opaque; humeral region of praescutum restrictedly bright yellow; scutellum obscure orange-yellow, parascutella dark. Pleura black, more heavily gray pruinose, conspicuously variegated with yellow, arranged as follows: Dorsopleural region; dorsal anepisternum; posterior ventral sternopleurite; dorsal and ventral pteropleurite, and on the metapleura. Halteres conspicuously light sulphur yellow, the base of stem restrictedly darkened. Legs with the coxae black, sparsely pruinose; remainder of legs black. Wings (Fig. 31) subhyaline, the prearcular field slightly more yellowish; veins pale brown. Venation: Sc moderately long, Sc_1 ending a short distance before fork of Rs , Sc_2 far from its tip; R_{2+3+4} usually much longer than R_{2+3} , in cases the veins subequal; cell M_2 open by the atrophy of m ; $m-cu$ a short distance before the fork of M , this distance slightly variable; Anal veins divergent, vein 2nd A strongly convex.

Abdomen black, the segments patterned with yellow, on the more basal segments restricted to the posterior lateral angles; larger and more conspicuous on the subterminal segments, forming complete crossbands at the posterior borders; hypopygium relatively large, chestnut brown to darker brown. Male hypopygium (Fig. 37) with the basistyle, b , produced slightly beyond the point of insertion of the dististyles as a low obtuse glabrous lobe or flange. Both dististyles relatively small and simple, the outer style, od , glabrous, almost parallel-sided, its apex blackened and obliquely truncated, the outer upper angle subacute; inner dististyle, id , slightly longer, appearing as a flattened blade, its apex obtuse, the setae small, distributed at apex and along the lower or cephalic edge. Gonapophyses, g , appearing as simple blackened rods with acute tips, the outer pair strongly sinuous; inner apophyses more nearly straight with their bases dilated.

Holotype, ♂, Arizona Creek, Station 1, 6,790 ft., July 2, 1941 (C. P. Alexander). *Allotopotype*, ♀, pinned with the type. *Paratopotypes* 6 ♂ ♀, pinned with the types; numerous additional paratypes, 6,790-6,800 ft., July 1-8, 1941 (C. P. & M. M. Alexander; W. H. Harrison); July 5, 1942 (C. P. Alexander).



(Symbols: b, basistyle; g, gonapophysis; id, inner dististyle; od, outer dististyle; p, phallosome.)

The present very distinct crane-fly belongs to the typical group of the subgenus, now known to be represented by several species distributed throughout the Holarctic Region. In our fauna, the only related species is *Erioptera* (*Psiloconopa*) *cramptonella* (Alexander, 1931), of eastern Canada, which differs in the larger size, venation, and in the very different male hypopygium. In its open cell M_2 , the present fly agrees more closely with *E. (P.) pusilla* (Schiner, 1865) of Europe, and *E. (P.) verna* (Alexander, 1920), of Japan.

In recent years it has become increasingly evident that it will be difficult or impossible to maintain as distinct certain subgenera of *Erioptera*, such as *Ilisia* Rondani, *Hoplolabis* Osten Sacken, and *Psiloconopa* Zetterstedt. I have

Fig. 30. *Gonomyia* (*Gonomyia*) *vafra* sp. nov.; venation.

Fig. 31. *Erioptera* (*Psiloconopa*) *shoshone* sp. nov.; venation.

Fig. 32. *Erioptera* (*Ilisia*) *bispinigera* Alexander; venation.

Fig. 33. *Erioptera* (*Ilisia*) *manitobensis* Alexander; venation.

Fig. 34. *Erioptera* (*Ilisia*) *rainieria* Alexander; venation.

Fig. 35. *Erioptera* (*Ilisia*) *zukeli* Alexander; venation.

Fig. 36. *Gonomyia* (*Gonomyia*) *vafra* sp. nov.; male hypopygium.

Fig. 37. *Erioptera* (*Psiloconopa*) *shoshone* sp. nov.; male hypopygium.

Fig. 38. *Erioptera* (*Ilisia*) *bispinigera* Alexander; male hypopygium.

Fig. 39. *Erioptera* (*Ilisia*) *rainieria* Alexander; male hypopygium.

Fig. 40. *Erioptera* (*Ilisia*) *dorothea* Alexander; male hypopygium.

Fig. 41. *Erioptera* (*Ilisia*) *zukeli* Alexander; male hypopygium.

discussed this problem in other papers and it seems virtually certain that eventually all three groups will be reduced to a single name, the oldest being *Psiloconopa*. In this particular subgenus several very distinct groups of species are found, some of which are well represented in the Rocky Mountain region.

Erioptera (Ilisia) bispinigera Alexander, 1930.—Arizona Creek, Station 1, 6,790 ft., July 2-15, 1941. Hitherto known only from the unique type specimen from Montana. The wing venation is shown (Fig. 32). Male hypopygium (Fig. 38) with the basistyle, *b*, at apex produced into a small conical point that bears several very long setae; mesal face of style near base with a pale fleshy lobe provided with several short setae; remainder of style with scattered elongate setae. Outer dististyle, *od*, a blackened blade, the stem relatively short, the distal two-thirds expanded into an oblique spatula, its outer margin with parallel rows of subappressed comb-like teeth. Inner dististyle, *id*, shorter and smaller, outer or lateral margin produced into two powerful black spines, the more basal one slightly larger, both spines slightly recurved; surface of style with numerous conspicuous setae. Phallosome, *p*, consisting of a powerful blackened plate on either side, broad at base, at near midlength with the outer portion produced into a long slender spinous rod, the tip acute, the outer margin before apex with a few appressed teeth; on mesal edge at point of narrowing of style with a smaller knoblike projection that is tipped with numerous short blackened spines to produce a macelike appearance.

Erioptera (Ilisia) margarita Alexander, 1919.—A few specimens taken along Pilgrim Creek, near Moran, 6,800 ft., July 5, 1942 (*M. M. Alexander*). One male shows an interesting abnormality of venation. The right wing (mounted on slide) has cell M_2 open by the atrophy of the basal section of vein M_3 , producing a *Mesocyphona* type of venation; the left wing has the cell open by the atrophy of *m*, producing the normal *Erioptera* type.

Erioptera (Ilisia) manitobensis Alexander, 1929.—Arizona Creek, Station 1, July 1-8, 1941; numerous. The wing venation is shown (Fig. 33).

Erioptera (Ilisia) rainieria Alexander, 1943.—One male, Cascade Trail, Station 4, 8,200 ft., July 9, 1941. This was in the alpine fir-whitebark pine-heath association discussed before.

I had hitherto referred this species and the more southern *dorothea* to the subgenus *Hoplolabis* Osten Sacken but it now appears preferable to place both in the older subgenus *Ilisia* Rondani. If *Hoplolabis* is to be recognized as a subgenus distinct from *Ilisia* or *Psiloconopa*, it must be strictly on the basis of the spurred or divided cell 1st M_2 , which would restrict the group to the subgenotype, *armata* Osten Sacken, 1859, and two further species, *bipartita* Osten Sacken, 1877, and *asiatica* Alexander, 1919. At best it would appear that *Hoplolabis* may be maintained as a weak subgenus for convenience only.

The differences between *dorothea* and *rainieria* are best shown in the structure of the male hypopygium, as follows:

E. (I.) dorothea Alexander, 1914. Male hypopygium (Fig. 40); apical lobe of basistyle, *b*, very slender, extending caudad beyond the level of the

outermost arm of the outer style. Outer dististyle, *od*, entirely blackened, the three arms unequal, the central one short, about one-half the length of the outer; outer arm with microscopic spinulae; lower arm longer and more slender, the tip obtuse. Inner dististyle, *id*, a long slender rod, entirely pale, strongly bent at midlength to appear more or less boomerang-shaped, the tip very obtuse. Gonapophyses, *g*, blackened, on either side with a subquadrate plate, from the cephalic lateral angle of which arises a long slender spine that is bent on its base, directed caudad and slightly mesad, very gradually narrowed to the acute blackened tip; basal plate at outer lateral angle produced into two blackened teeth. (Colorado—New Mexico).

E. (I.) rainieria Alexander, 1943. Male hypopygium (Fig. 39); apical lobe of basistyle, *b*, slender, extending caudad about to the level of the outermost arm of outer dististyle. Outer dististyle, *od*, entirely blackened, with a very short base that is produced into three short arms of approximately the same shape; outer arm obtuse at tip, its outer surface with appressed acute spinulae, its lower surface merely crenulate; central arm of about the same length, more narrowed outwardly, the lower surface crenulate; lower arm shorter and more strongly curved, thickest at near midlength, thence narrowed to a stout acute point. Inner dististyle, *id*, a pale stout clavate lobe, strongly widened on distal half. Gonapophyses, *g*, blackened, with two principal arms, a more basal slender spine directed laterad, and a flattened outer blade that is twisted at near midlength. Ninth tergite large, its caudal margin with a deep U-shaped notch, the lateral lobes more broadly obtuse. (Wyoming—Washington). The wing venation is shown (Fig. 34).

E. (I.) zukeli Alexander, 1940.—Arizona Creek, 6,790 ft., June 1-8, 1941; July 5, 1942. Hitherto known only from the unique female type from Idaho. The present material agrees closely with the type except that in most specimens the dark pattern of the wing along vein *Cu* is much more restricted and does not involve cell *M*. The wing-venation is shown (Fig. 35). Male hypopygium (Fig. 41) about as shown. Outer dististyle, *od*, unequally trilobed, with two primary flattened blades, with a third smaller lobe on the upper margin of the lower of these blades; outer blade microscopically roughened on outer face, the inner blade more nearly smooth. Inner dististyle, *id*, entirely pale and fleshy. Gonapophyses, *g*, appearing as powerful curved lateral horns that narrow to acute spinous points, the inner portion close to the midline produced caudad into smaller acute horns; outer margins of lateral horns with microscopic appressed denticles, the inner margin in cases with a more or less distinct denticle.

Cryptolabis (Cryptolabis) molophiloides Alexander, 1943.—Jenny Lake, 6,800 ft., July 13, 1941 (*C. P. Alexander*); part of the type series. As previously indicated, this series was taken in the dry evergreen forests near the camp at the lake, the tree species being chiefly lodgepole pine, Douglas fir and alpine fir; no streams or other wet areas were present other than the lake which was some distance away. The significance of these remarks lies in the fact that although we have no definite knowledge of the immature stages, we have several reasons to believe that the larvae of members of the genus are

strictly aquatic. Where the immature stages of the present fly occur remains very much in question.

Ormosia (Ormosia) absaroka Alexander, 1943.—Twogwotee Pass, Station 6, 9,650 ft., July 9, 1942; abundant along small mountain torrents that were fed wholly or in part by melting snow; associated with *O. (O.) paradisea* Alexander.

Ormosia (Ormosia) albertensis Alexander, 1933.—Arizona Creek, 6,790 ft., July 4, 1942; Jenny Lake, Station 5, 6,780 ft., July 3, 1941; Leigh Lake, Station 5, 6,870 ft., July 10-12, 1941; Indian Paintbrush Canyon, 7,500-8,000 ft., July 13, 1941.

Ormosia (Ormosia) dedita Alexander, 1943.—Hidden Falls, 6,900 ft., July 8, 1942; Jenny Lake, Station 5, July 6, 1941; Leigh Lake, Station 5, July 10-12, 1941.

Ormosia (Ormosia) fusiformis (Doane, 1900).—Jenny Lake, 6,790 ft., July 6, 1941.

Ormosia (Ormosia) hallahani Alexander, 1943.—Arizona Creek, 6,790 ft., July 4, 1942; Leigh Lake, Station 5, 6,870 ft., July 12, 1941; Indian Paintbrush Canyon, 8,000 ft., July 13, 1941. This very distinct fly is evidently widely distributed in the northern Rockies; I have seen it from the Big Horn Mountains, Wyoming, and the Black Hills, South Dakota.

Ormosia (Ormosia) manicata (Doane, 1900) (*deviata* Dietz, 1916; *fuscopyga* Alexander, 1924).—Moran bog, 6,800 ft., July 2-5, 1941; Jenny Lake, near camp, 6,790 ft., July 1, 1941.

Ormosia (Ormosia) megarhabda Alexander, 1943.—Arizona Creek, Station 1, 6,790 ft., July 8, 1941.

Ormosia (Ormosia) onerosa Alexander, 1943.—Arizona Creek, Station 1, 6,790 ft., July 4, 1942.

Ormosia (Ormosia) paradisea Alexander, 1920 (*garretti* Alexander, 1926).—Twogwotee Pass, Station 6, 9,650 ft., July 9, 1942; taken by sweeping fir and spruce along a small, clear mountain stream, very common.

Ormosia (Ormosia) sentis Alexander, 1943.—Arizona Creek, Station 1, 6,790 ft., July 4, 1942.

Ormosia (Ormosia) tetonica sp. nov.—Allied to *innocens*; general coloration blackened, heavily pruinose; antennae short, black throughout, basal flagellar segments subglobular; halteres black, the knobs obscure yellow; legs black, the femoral bases more reddish brown; wings yellow, restrictedly patterned with brown; macrotrichia of cells unusually sparse, restricted to outer cells of wing; cell 1st M_2 closed; vein 2nd A gently sinuous; male hypopygium with the ninth tergite complex, produced into two slender lobes that are separated by a rounded notch; dististyle a heavily blackened mace-like structure, provided with several blackened denticles.

♂. Length, about 4.2-4.5 mm.; wing, 5-5.6 mm.; antenna, about 1 mm.

♀. Length, about 5 mm.; wing, 6.8 mm.

Rostrum and palpi black. Antennae relatively short, black throughout; basal flagellar segments short-oval to nearly globular, the outer six or seven segments oval and much more slender; terminal segment elongate, more than one-half longer than the penultimate. Head blackened, heavily gray pruinose; anterior vertex wide.

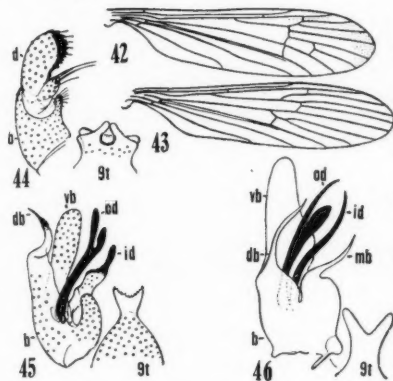


Fig. 42. *Ormosia (Ormosia) tetonica* sp. nov.; venation.

Fig. 43. *Molophilus (Molophilus) harrisoni* sp. nov.; venation.

Fig. 44. *Ormosia (Ormosia) tetonica* sp. nov.; male hypopygium.

Fig. 45. *Molophilus (Molophilus) harrisoni* sp. nov.; male hypopygium.

Fig. 46. *Molophilus (Molophilus) nitidus* Coquillett; male hypopygium.

(Symbols: *b*, basistyle; *d*, dististyle; *db*, dorsal lobe of basistyle; *id*, inner dististyle; *mb*, mesal lobe of basistyle; *od*, outer dististyle; *yv*, ventral lobe of basistyle; *t*, tergite.)

Pronotum black, sparsely gray pruinose; anterior pretergites obscure brownish yellow, poorly differentiated. Mesonotum blackened, heavily pruinose, the praescutum with three brownish black stripes; median stripe broad and conspicuous, not reaching the suture behind; lateral stripes narrow and poorly indicated; pseudosutural foveae and tuberculate pits black, the latter lying in front of the level of the latter. Pleura, including dorsopleural membrane, dark gray. Halteres with stem blackened, knobs abruptly obscure yellow. Legs with the coxae and trochanters black, sparsely pruinose; remainder of legs brownish black to black, the femoral bases more reddish brown. Wings (Fig. 42) with the ground color yellowish, restrictedly but conspicuously patterned with pale brown, as follows: Cord; outer end of cell 1st M_2 ; origin of R_5 ; paler washes along veins beyond cord and in outer portions of Anal cells, especially cell 1st A ; veins brown. Macrotrichia of cells unusually sparse (shown in figure by stippling), restricted to cells beyond cord and chiefly to outer ends of these cells, especially in the outer radial and medial fields. Venation: Sc_1 ending about opposite one-third to one-half R_{2+3+4} ; R_2 usually less than its own length beyond fork of R_{2+3+4} , in cases at or even shortly before the fork; vein R_3 a little upcurved at apex; cell 1st M_2 closed, subequal in length to vein M_4 beyond it; $m-cu$ gently sinuous, close to the fork of M ; vein 2nd A gently sinuous, cell 2nd A widest before midlength.

Abdomen, including hypopygium, black. Male hypopygium (Fig. 44) with the tergite, 9t, unusually complex, consisting of a lower and an upper plate, the latter produced into two slender lobes that are separated by a con-

spicuous U-shaped notch, the tips of the lobes almost touching and thus closing the notch or virtually so. Basistyle, *b*, with mesal face near apex bearing an oval lobe provided with several long setae. Dististyle, *d*, a massive blackened structure, the apex and mesal face heavily blackened and produced into several teeth to produce a mace-like appearance; on mesal face at near one-third the length bearing a small dusky lobe that is provided with several setae, two of which are of unusual length, much longer than the lobe itself. Gonapophyses appearing as flattened plates with obtuse margins.

Holotype, ♂, Arizona Creek, Station 1, 6,790 ft., July 4, 1942 (*M. M. Alexander*). *Allotopotype*, ♀, with the type. *Paratopotypes*, 33 ♂♂, with the type (*C. P. & M. M. Alexander*); 5 ♂♀, July 1-8, 1941 (*C. P. Alexander*); the main series was taken while flying close to the low overhanging banks of the stream, just above the water; one week later they had completely disappeared.

The present fly is very distinct from the two eastern Nearctic species that are most nearly allied, *Ormosia* (*Ormosia*) *apicalis* Alexander, 1911, and *O. (O.) innocens* (Osten Sacken, 1869). The great reduction in number of macrotrichia in the wing cells is particularly noteworthy. In both allied species these trichia are much more abundant and are distributed over virtually the entire wing surface, as is common in the genus. From their reduction in number in the present fly it would seem reasonable to expect that an *Ormosia* wholly lacking macrotrichia in the wing cells may be discovered or that such species have already been described but are now placed in the closely related genus *Erioptera*, based on the lack of such trichia in the wing cells. It is thus obvious that the generic distinctions between *Ormosia* and *Erioptera* are not as well-marked as had formerly been believed.

Whether the present fly and its two Nearctic relatives fall in the subgenus *Scleroprocta* Edwards, 1938, remains somewhat in question but probably will be found to be the case. The chief characters of this subgenus, other than the ones confined to the male sex, are the glabrous postnotum and the cephalic position of the tuberculate pits of the praescutum which lie before the transverse level of the pseudosutural foveae. However, it should be noted that various other groups of *Ormosia* similarly have the above mentioned characters, these including the *nigripila* group and the species that center about *O. (O.) prava* Alexander, 1940, including the western Nearctic *O. (O.) hallahani* Alexander. Whether it is advisable to erect subgenera for these various isolated groups of *Ormosia* seems somewhat questionable to me at the present time. It appears certain that there will be some notable discoveries in this genus in the Indo-Chinese region that may still further complicate this matter.

Molophilus (*Molophilus*) *colonus* Bergroth, 1888.—Moran bog, Station 2, 6,800 ft., July 2-5, 1941.

Molophilus (*Molophilus*) *falcatus* Bergroth, 1888.—Jenny Lake, Station 5, 6,780 ft., July 3, 1941; Leigh Lake, Station 5, 6,870 ft., July 10-12, 1941; Indian Paintbrush Canyon, 7,500 ft., July 13, 1941.

Molophilus (Molophilus) harrisoni sp. nov.—Belongs to the *gracilis* group and subgroup; allied to *nitidus*; general coloration dark brown or brownish black, sparsely pruinose; head dark brown; pronotal scutellum and the pretergites variegated with yellow; halteres pale yellow; legs brownish black; wings with a strong blackish tinge; R_{2+3} and basal section of R_{4+5} long, petiole of cell M_3 short; male hypopygium with the ninth tergite terminating in a flattened-depressed plate, its caudal margin with microscopic teeth; mesal lobe of basistyle obtuse; inner dististyle a blackened rod, narrowed on outer portion and provided with abundant blackened spines; aedeagus long and slender.

♂. Length, about 3.8-4.2 mm.; wing, 4-4.5 mm.; antenna, about 1-1.1 mm.

♀. Length, about 4.5 mm.; wing, 4.8 mm.

Rostrum and palpi black. Antennae relatively short, black throughout; flagellar segments oval; longest verticils slightly exceeding the segments in length, chiefly unilaterally distributed. Head dark brown.

Pronotum dark brown, the lateral borders of scutellum and the pretergites obscure yellow. Mesonotum dark brown to brownish black, the surface sparsely pollinose; scutellum dark. Pleura dark brown, sparsely pruinose; dorsopleural membrane obscure yellow to brownish yellow. Halteres pale yellow. Legs brownish black. Wings (Fig. 43) with a strong blackish tinge, the prearcular field a trifle more brightened; veins and macrotrichia brownish black. Venation: Sc_1 ending about opposite R_2 ; R_{2+3} long, a trifle exceeding basal section of R_{4+5} ; cell M_3 deep, its petiole variable in length, from subequal to *m-cu* to one-half longer than this element; vein 2nd *A* relatively short, gently sinuous, ending before level of *m-cu*.

Abdomen, including hypopygium, black. Male hypopygium (Fig. 45) with the ninth tergite, *9t*, conspicuous, narrowed outwardly, terminating in a flattened-depressed plate, the caudal margin of which is concave and irregularly toothed. Basistyle, *b*, with the dorsal lobe, *db*, at apex narrowed into a cylindrical yellow rod that terminates in a powerful black spine, at base of latter with several conspicuous setae; ventral lobe, *vb*, long, clavate; mesal lobe short and obtuse. Outer dististyle, *od*, an elongate blackened rod, unequally bifid at tip, both lobes obtuse at their tips. Inner dististyle, *id*, a shorter black rod, stout on basal half, the outer portion conspicuously narrowed, the surface of outer portion with abundant blackened spinous points; surface of enlarged basal portion with scattered setae. Aedeagus unusually long and slender.

Holotype, ♂, Arizona Creek, Station 1, 6,790 ft., July 8, 1941 (*W. H. Harrison*). *Allotopotype*, ♀, pinned with type. *Paratopotypes*, 6 ♂ ♀, July 1-8, 1941 (*C. P. Alexander & W. H. Harrison*); 1 ♀, July 4, 1942 (*M. M. Alexander*).

This very interesting and distinct fly is named in honor of Mr. Walter H. Harrison, who has participated in virtually all of our collecting trips during the past ten years. The nearest ally is the more western *Molophilus (Molophilus) nitidus* Coquillett, 1905, which differs in the still larger size (*Holotype*, male, length, 4.5 mm.; wing, 6.2 mm.), more intensely black coloration

of the body and appendages, and, especially, the structure of the male hypopygium. The type of *nitidus* was taken at Fieldbrook, California, May 18, 1903, by H. S. Barber and is preserved in the United States National Museum (Type No. 8347). I am greatly indebted to Dr. Henry Townes for making a slide mount of the hypopygium of this type and sending me a drawing that shows the essential structures. From this (Fig. 46) it may be noted that the ninth tergite, *9t*, terminates in a simple furcula, without denticles; both the dorsal, *db*, and mesal, *mb*, lobes of the basistyle, *b*, are produced into long slender spines of approximately the same shape. The upper branch of the outer dististyle, *od*, likewise is a long slender sinuous rod that narrows gradually to the acute tip. The drawing further indicates that the aedeagus is quite different in shape from that of *harrisoni*, near its apex bearing a lateral spur or branch immediately before the decurved tip. From this figure of the type I have determined that *nitidus* is represented in my own collection from northern California and Oregon and that there is a still different undescribed species in extreme southern California.

Molophilus (Molophilus) perflaveolus Alexander, 1918.—Arizona Creek, Station 1, July 5, 1941; Snowshoe Cabin, Wister Draw, at foot of Death Canyon, 6,800 ft., July 14, 1941. The species is exceedingly close to *M. (M.) auricomus* Alexander, 1926, of the southeastern United States.

Molophilus (Molophilus) rostriferus Alexander, 1943.—Twogwotee Pass, 9,650 ft., July 9, 1942; in swampy meadows near Jackson Lake, 6,800 ft., July 5, 1942; part of type material.

***Molophilus (Molophilus) spiculatus sigmoideus* subsp. nov.—**

Very similar to typical *spiculatus* Alexander, 1918, differing only in slight hypopygial details. The outer dististyle has the conspicuous sigmoid shape in both races but in the present fly the inner style is shorter and broader, particularly across its base. In typical *spiculatus* the blackened outer portion is approximately one-half the total length of the outer style and the spiculae of the surface are more sparse, particularly on basal portion and sides, being best developed on outer surface and on outer half of lower edge. In the present race, the blackened outer portion of the inner style is only about one-third the length of the outer style while the spiculae are more abundant and more evenly distributed, occurring virtually to the base.

Holotype, ♂, Cascade Trail, Grand Tetons, 8,500 ft., July 9, 1941 (*C. P. Alexander*). *Paratopotypes*, ♂ ♀. *Paratypes*, ♂ ♀, Moose Ponds, near Jenny Lake, 6,700 ft., July 6, 1941; Leigh Lake, Station 5, 6,870 ft., July 10-12, 1941; Indian Paintbrush Canyon, 7,000-8000 ft., July 13, 1941; Twogwotee Pass, Station 6, 9,650 ft., July 9, 1942 (*C. P. Alexander*).

The classification of the western Nearctic members of the *gracilis* group, *pubipennis* subgroup, is fully as complicated and involved as is the condition in the species of eastern North America. Bergroth, in 1888, described from southern Alaska three species, *colonus*, *falcatus* and *paulus*, that, despite my inability to study the types now preserved in Finland, I feel have been correct-

ly identified. The species most in question is *colonus* and it seems certain that what Coquillett (Harriman Expedition Report, 1900) determined as this from Alaska and later from British Columbia, is not the true *colonus* but actually pertains to the new subspecies of *spiculatus* described above. This latter species has the wings unpatterned while Bergroth's description of *colonus* calls very definitely for a fly with marked wings. I have identified as *colonus* a species previously recorded (Alexander, 1943: 762) from the Yellowstone and represented in the Teton series. It appears further that *comatus* (Doane, 1900) is a synonym of *colonus*. *Molophilus squamosus* Alexander, 1919, from the extreme southern parts of California appears to represent a subspecies of *colonus*. The present fly, *spiculatus*, has the outer dististyle of the male hypopygium more strongly sigmoid than any of these allied species. *Molophilus paulus* Bergroth, of which I have seen a broken male from the type locality (Sitka, Alaska) has the antennal structure and vestiture distinct from all of the above mentioned members of the *pubipennis* subgroup. Unfortunately, the abdomen of this specimen is broken and the hypopygium cannot be described.

Rhabdocoela of Wisconsin. II.¹

Morphology and Taxonomy of *Castrella pinguis*
(Silliman 1884) Fuhrmann 1900

Wayland J. Hayes, Jr.

The flatworm considered in this paper has already been reported from Monroe County, New York; Adams County, Pennsylvania; and Shenandoah, Giles, and Albemarle Counties, Virginia; and is now reported from Dane, Vilas, and Ashland Counties in Wisconsin. In spite of this relatively wide, known distribution and the ease—compared with other rhabdocoelae—with which it may be identified, there exists in the literature some confusion regarding its anatomy and classification. In this paper a complete description based entirely on original observations is presented as a basis for a critical discussion of the literature.

Description.—Body elongate, fairly slender, the sides subparallel for the greater part of the length of the animal; color sometimes brownish, usually a very dark grey or black with the unpigmented body wall forming a halo around the edge; pigment usually evenly distributed, sometimes concentrated around the pharynx; total length up to 2 mm. Epidermis 12-16 μ high dorsally, 6 μ or less ventrally, and 22 μ high anteriorly and posteriorly. Cilia about 10 μ long. Sensory hairs about 20 μ long present at the anterior and posterior ends. Weak adhesive cells present at the posterior end. Blunt rod-shaped rhabdites up to 15 μ long distributed abundantly in groups of 1-7 over the body surface and in packets beneath the epidermis in all parts of the body and especially in the spaces around the pharynx and posterior to the testes. Paired cerebral ganglia joined by a broad commissure set off on each side by an indentation of the anterior surface of the crescent-shaped brain. Eyes paired, black in color, about 28 μ in greater diameter, dorsal to the brain, and a little nearer to the sides of the body than to one another; each eye composed of a small, round anterior portion and a larger, oval or sometimes bilobed posterior portion connected to the former by a bridge of pigment. Protonephridia opening by paired pores placed lateral and slightly anterior to the common genital atrium. Digestive system typical; prominent pharynx doliiformis² leading by a short oesophagus provided by a ring of digestive glands into the sac-like enteron composed of a high columnar epithelium; enteron extending back nearly to the level of the genital pore. Testes large, smooth, compact, dorsal and median to the vitellaria, broadly spindle-shaped except where indented by the

¹ The first of this series of papers was published in the *American Midland Naturalist* 25(2):388-401, 1941. The two papers are part of a thesis submitted to the faculty of the University of Wisconsin in partial fulfillment of the requirements for the degree of doctor of philosophy.

² The expression "pharynx doliiformis" and other anatomical terms used in this paper are clearly defined by Breslau (1933).

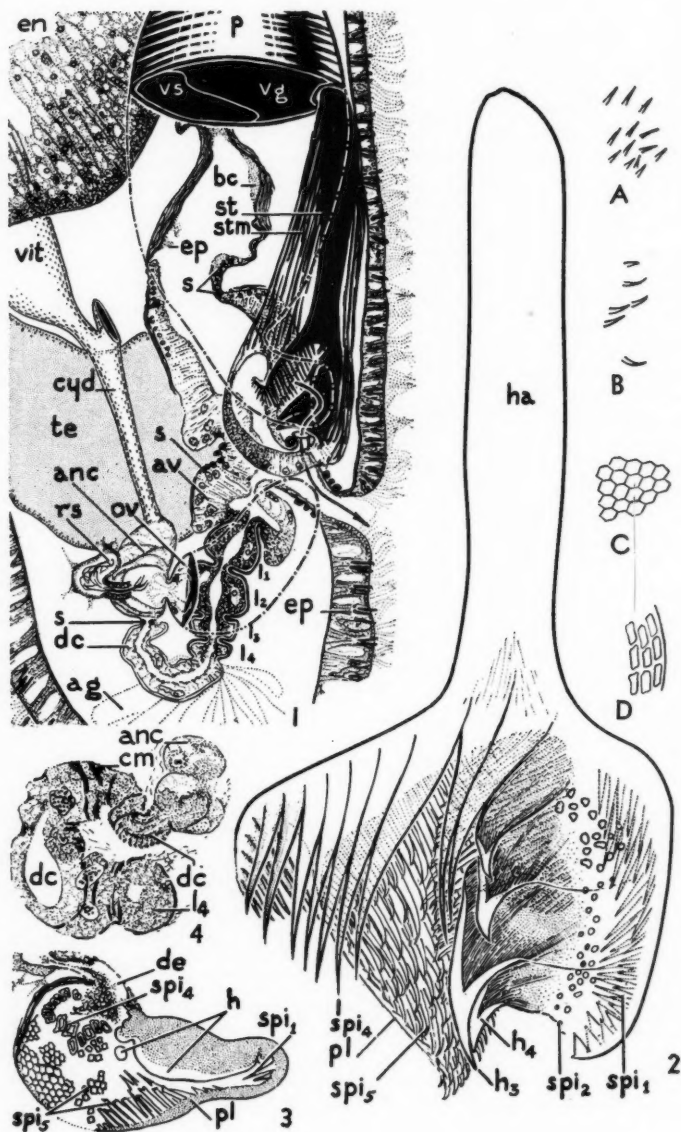
pressure of other organs, placed in the posterior body third, and gradually narrowed anteriorly to form the vasa deferentia. Vas deferens of each side directed anteriorly and mesially to unite with its counterpart in entering the anterior end of the penis bulb. False vesiculae seminales not observed. Vesicula seminalis and vesicula granulorum placed beside one another in the penis bulb; vesicula seminalis dorsal and median to the vesicula granulorum. Wall of the bulb composed of a single layer of rather thin circular muscle lying on a basal membrane. Bulbus gradually narrowed distally to form the widest and most proximal portion of the ductus ejaculatorius which with the succeeding duct-like portion has the lumen surrounded by glands whose secretion stains with Delafield's hematoxylin and presumably functions in the formation of spermatophores. Ductus ejaculatorius thin-walled distal to the glandular portion; the entrance to the stylet pouch ventro-lateral. Stylet a single, long, cylindrical handle bearing at its distal end a complicated plate folded upon itself along the sides and provided with a variety of spines so that the whole structure has (as Silliman observed) the appearance of a home-made broom; spines of six major sorts: (1) stout needle-like spines arising from quadrangular insertions and ranged in three more or less regular rows along the bottom of the trough formed by the folded plate at the base of the hooks; (2) a group of spines in the form of blunt tubercles ranged in a very irregular fashion between the spines of groups one and three, being actually nodules on the bases of the hooks; (3) a row of powerful solid hooks or thorns at least four in number placed edge to edge or overlapping and with distinct point and basal portions; (4) a group of long, strong, somewhat curved and flattened, hollow spines quadrangular in cross-section, placed in a single row along the dorso-lateral margin of the stylet, and set off from those of the next group by a spineless portion of the plate; (5) extremely fine, needle-like points square and hollow in cross-section, arising from hexagonal insertions over the entire remaining portion of the inner ventral surface of the plate; (6)³ small, hair-like points sparingly distributed over the outer surface of the plate and directed proximally or at right angles to the axis of the stylet; the sharp folding of the plate along the bases of the hooks and between the spines of groups four and five resulting in a flattening of the spinous portion of the resting stylet so that the hooks and the spines of group four lie over the other spines and appear to rise from two branches of the handle, the branches being optical sections of the two folds or actual branches if breaks have occurred along the folds; the hooks with points like rose thorns but raised on high bases so that the entire structure does not resemble a rose thorn closely; the lower part of the base of each thorn divided proximally into two branches between which the thorn just behind rises; the handle usually one and three-fourths times the length of the spinous plate, sometimes over twice as long; the entire stylet 75-160 μ long. Spinous plate formed first in young animals

³ The author has seen the spines of this sixth group after treatment of the stylet with KOH. Their relationship to the plate is believed to be as described, but just how this is to be harmonized with the fact that some of the outer surface of the plate serves for muscle attachment is not clear. It may be that they are cuticular "tendons" of the separate muscle fibers inserted on the cuticular plate.

ABBREVIATIONS USED

ag—accessory glands	ov—ovary
anc—antechamber	p—penis
av—atrial vestibule	pl—plate
bc—bursa copulatrix	rs—receptaculum seminis
cm—circular muscle	s—sphincter
cyd—common yolk duct	spi—spine
dc—ductus communis	st—stylet
de—ductus ejaculatorius	stm—stylet-muscle
en—enteron	te—testis
ep—epithelium	vg—vesicula granulorum
h—hook	vit—vitellaria
ha—handle	vs—vesicula seminalis
l—locule	

Figs. 1-4—*Castrella pinguis*: Fig. 1. Semi-diagrammatic view of the genital organs seen from the right side (The diagram was formed by superimposing camera lucida drawings of the sagittal serial sections composing slide U.S.N.M. no. 20635. Many of the organs are treated as optical sections and their histology shown. The ovary and penis have been removed in part. Their position is shown by construction lines. A bristle is shown as passing from the position of the ductus ejaculatorius, through the male genital canal, and finally out of the common genital pore.) ($\times 410$); Fig. 2, stylet seen from the ventro-lateral surface, A and B—spines of type 6, C—hexagonal insertions of spines of type 5 on the basal plate, D—quadrangular insertions of spines of type 1 (stylet and details drawn to the same scale) ($\times 940$); Fig. 3, transverse section of the stylet showing some of the spines and, like the preceding figure, with the ventro-lateral surface up. (Slide 474—16, $\times 940$); Fig. 4, sagittal section of a part of the female genital tract (from slide 506—a—4 lent by Dr. Kepner from his collection, $\times 940$).



and the handle afterwards. Handle of the stylet inserted in a pocket of the male genital canal and heavily sheathed by a cone of protractor muscle fibers attached in part to the plate of the stylet and in part to the wall of the male genital canal and serving to push the stylet out and expose the spines. Spinous plate with the distal half exerted into the male genital canal beside the opening of the ductus ejaculatorius. Proximal part of the male genital canal muscular, without an epithelial lining, and separated from the distal part by a more or less definite constriction; distal part of the canal with a columnar epithelium similar to that of the superior genital atrium. Male genital canal opening on the anterior surface of the very small inferior genital atrium; the latter set off above and below by sphincters. Sperm about $100\ \mu$ long, thread-like, and with two fine flagella attached near one end. Bursa copulatrix a muscular sac with stem and bulbar portions not clearly defined and highly variable; wall composed of a layer of circular muscle lying on a basal membrane and sparingly overlaid by longitudinal muscle strands; the two muscle layers forming a spiral pattern over the bulb of the bursa; proximal border of the bursa held out by a pair of long muscles attached to the body wall near the base of the pharynx; heavy basal membrane formed in young specimens by the epithelium which later nearly or quite degenerates; total length of the bursa usually $100\text{--}200\ \mu$; the lumen usually filled by 1-4 spermatophores. Spermatophore flask-shaped, from 100 to $220\ \mu$ long; neck of the structure composed of heavier cuticle than the irregularly folded bulb and with a heavy ring of cuticle more or less divided into nodules guarding the opening; outside diameter of the opening about $20\ \mu$. Ovary compact, placed in the very posterior end of the body and directed anteriorly and dorsally or placed a little more anteriorly and directed backward and dorsally depending on the movements of the animal. Tunica propria of the distal part of the ovary embracing a spherical segment filled with tunica cells and continuous by a narrow constriction with the antechamber which represents the most proximal part of the ductus communis. Receptaculum seminis an irregular, often lobed sac rising by a short, thick-walled duct of narrow lumen from the dorsal surface of the antechamber on the same side as the ovary; stem of the receptaculum seminis defined by fine circular muscles. Vitellaria simple, strap-shaped or cylindrical, extending laterally from the posterior part of the pharynx to the posterior part of the enteron where each vitellarium continues mesially and posteriorly as a duct to meet its counterpart in forming the common yolk duct, which in turn enters the more distal part of the antechamber; proliferating cells of the vitellaria forming only slight elevations on the surface of the glands. Ductus communis composed of four portions as arranged from the ovary to the atrium: (1) the antechamber; (2) a narrow duct rather completely covered by a thin layer of circular muscle and grading imperceptibly or by a swollen portion into (3) a well-defined, tube-like portion taking a good stain with Delafield's hematoxylin and receiving in its most distal part the long granular ducts of many one-celled accessory or colloidal glands; (4) a series of four distinct locules the most distal of which opens into the vestibule of the superior genital atrium. Cells of the antechamber arranged in a lamellar fashion to form a thick but irregular wall. Most distal locule cone-shaped and almost as large as the second locule; three proxi-

mal locules spherical or somewhat flattened and graduated in size, the most distal being largest; all of the locules often modified in shape by the pressure of other organs but retaining their identity constantly; locules covered on the outside by a very heavy basal membrane and each locule lined by a few cells with well defined, large, vesicular nuclei; the cells usually taking a deep color with Delafield's stain. Accessory gland bodies forming a large mass in the posterior end of the body behind the testes. Atrial vestibule similar to the superior genital atrium in histology but set off from it by a constriction controlled by inner circular and outer longitudinal muscles crossing one another at an angle so as to form an effective and highly mobile sphincter. Superior genital atrium, when not holding an egg, usually small, little bigger than the vestibule and much smaller than the bursa copulatrix; the empty atrium lined by a high columnar epithelium; epithelium of the egg-filled atrium extremely flattened so that only the much depressed nuclei are easily visible. Superior genital atrium receiving the female genital canal on its posterior surface and the bursa anteriorly. Portion of the superior genital atrium just above the pore to the inferior atrium cut off from the remaining, anterior portion by a muscle system similar to that cutting off the vestibule posteriorly. Genital pore provided with glands whose prominent ducts packed with granules of secretion up to $10\ \mu$ in diameter radiate laterally and posteriorly from the opening. Egg brown in color, ovate, the narrow end drawn out into a curved somewhat flexible stalk; stalk mostly solid but usually with a few hollow spaces particularly in the more distal part; egg, excepting the stalk, measuring about $164 \times 124\ \mu$; stalk more variable in length, usually about $144\ \mu$ long and $6\ \mu$ thick but with some constrictions along the length. Chromosome number: $n=2$, $2n=4$. Chromosomes described by Ruebush (1938).

Specimens.—U.S. National Museum number 20634 taken from Lake Mendota, Madison, Wisconsin; and U.S. National Museum number 20635 and the slides of series 474 in the author's collection all taken from Mann Lake Drain at its intersection with Vilas County Highway M about two and a half miles from Trout Lake, Wisconsin.

Distribution.—*C. pinguis* has been collected from University Bay of Lake Mendota and from the Yahara River in Madison, Wisconsin (October 1939 and 1940 and May 1941); from various lakes and waterways in Vilas County, Wisconsin as follows: State Forestry Bog near Trout Lake, Manitowish River at its intersection with County Trunk Highway K, Mann Lake Drain at its intersection with County Trunk Highway M, Black Oak Lake, High Lake, Lac Vieux Desert, and Presque Isle River at Winegar, Wisconsin (July 1 to August 20, 1941 inclusive); and from Bad River in Copper Falls State Park near Mellen, Wisconsin (August 10, 1941).

Differential diagnosis.—Body usually darkly pigmented, up to 2 mm. in length; eyes bilobed; testes in the posterior body third; penis bulbus separate from the stylet-sheath; stylet with five distinct sorts of free spines and one other group of spine-like structures; spermatophores present; bursa copulatrix flask-shaped; female genital tract with a peculiar morphology including four

locules of constant structure; common genital atrium divisible into superior and inferior parts of which the former receives the female tract and serves as a uterus while the latter receives the male tract; egg provided with a stalk; chromosome number: $n=2$, $2n=4$.

Discussion.—The author is deeply grateful to Dr. William A. Kepner who lent all the original slides upon which the excellent paper, Kepner and Gilbert, 1931, was based. The author has been fortunate in having an unlimited supply of animals and of being able to demonstrate by special techniques certain structures which Kepner and Gilbert overlooked in their limited supply of material but which can now be made out in their slides. Especially useful was the treatment of total mounts with 5% KMnO_4 followed by normal HCl to completely remove the dense body pigment. Incidentally this treatment does not affect the eye pigment, showing that it is of a different chemical composition. This was also true of other rhabdocoeles so treated.

In spite of the great variety of configurations attributed to the stylet of the European *Castrella truncata* or of species said to be synonymous with it (Hofsten 1910), the American form is remarkably constant in morphology and has now been shown to be a distinct species. All the European workers have either overlooked the plate bearing a tremendous number of small spines or, which is more likely, the European form lacks this structure. Further, the number and morphology of the large hooks, the relative length of the handle, the total length of the stylet, the size of the testes, and several smaller features mentioned in the description serve to distinguish the American form from all available descriptions of the most closely related species, *C. truncata*.

Since the American form has been found so widely distributed and very common in the United States, it is felt that we are probably dealing with the species described by Silliman from Blodgett's Creek, Monroe County, New York. This is made almost certain by material collected from pools of Lake Ontario inlets near Rochester by Dr. Frederick F. Ferguson. Dr. Ferguson has kindly presented to the author study-drawings and fixed specimens of animals from this source which are indistinguishable from the material found in Wisconsin. The present description is more complete than Silliman's, but it contradicts his in only minor particulars such as the point of entrance of the vitellarian ducts into the female genital tract and the presence of a receptaculum seminis. Since Silliman's microscopic equipment can not have been as good as that now available, the differences are not considered important.

It must be noted, further, that Graff's description (1911 p. 49-51, pl. 3 f. 39-41 and 1913 p. 126-128 f. 129, 130) of *C. "pinguis"* contradicts Silliman's clear description in every important detail. Since we now know that a species indistinguishable from the one described by Silliman actually occurs in America over a wide range, it becomes evident that Graff was working with a different form or confused two forms. Since the name *pinguis* is occupied the name *Castrella graffi* nomen novum is proposed for Graff's animal.

In conclusion, the history of this species may be summarized as follows:

CASTRELLA PINGUIS (Silliman)

- Vortex pinguis* Silliman 1884, p. 65, pl. 4, fig. 11-16. [Type locality: Blodgett's Creek, Rochester, Monroe County, New York]. Girard 1893, p. 206.
- Castrella pinguis* (Silliman). Fuhrmann 1900, p. 726, 728. Kepner and Gilbert 1931, p. 169.
- Castrella truncata* (Abildgaard) Fuhrmann [unnamed "American variety"] Kepner and Gilbert 1931, p. 169-177, fig. 1-5. Ruebush 1938, p. 323, fig. 1-a. Ferguson, Stirewalt, Brown, and Hayes 1939, p. 275, 277.
- [non] *Jensenia pinguis* (Silliman). Graff 1910, p. 947. Graff 1911, p. 49, pl. 3, fig. 39-41. Stringer 1918, p. 348, fig. 618.
- [non] *Castrella pinguis* (Silliman). Graff 1913, p. 126, fig. 129, 130.

A few details of the morphology of *C. pinguis* will now be discussed.

The supposition that the spermatophores are formed in the proximal part of the ductus ejaculatorius in *C. pinguis* is based upon the facts that this part of the ductus contains a space similar in shape to a spermatophore, that the walls of this space are lined by glands, and that the secretion of these glands takes a characteristic stain with various dyes, especially Delafield's hematoxylin, which stain is repeated in the wall of the spermatophores regularly found stored in the bursa copulatrix.

The placement of the muscles on the stylet indicates that it not only may be pushed out of the male genital canal but also that the spinous plate is opened up so that the spines are directed outward like the bristles of a brush.

The division of that part of the ductus communis between the antechamber and the proximal locule into two regions may be very clear or very indistinct. Also that part just proximal to the locules is often corrugated, probably by the constriction of circular muscles, so that it comes to resemble the locules in shape. These two regions may always be distinguished, however, by the heavier basal membrane of the locules which causes the locules to retain their identity while the other annulations are temporary.

When *Castrella pinguis* deposits eggs in a clean glass vessel, each egg is attached lightly by its stalk with a very small amount of mucus secreted by the worm. The body of the egg is thus held clear of the surface.

Fixed total mounts and serial sections of animals containing eggs are available. All show the body of the egg lying in the common genital atrium. In some specimens the egg stalk also lies in the atrium directed toward the vestibule; in others the egg stalk extends a variable distance into the ductus communis. One slide shows an egg known to be less than one half hour old, the stalk of which extends into the fourth locule of the ductus communis. There is every indication, including its normal curvature, that the egg stalk is formed in and molded by the ductus communis.

Contrary to some statements in the literature, the epithelium of the superior genital atrium does not, except perhaps in very senile animals, degenerate as a result of containing an egg. This epithelium, as shown by stained sections of fixed, egg-bearing worms, remains intact through greatly stretched. Further, when egg-bearing worms were isolated in depression slides and later each one fixed when it was observed to have laid its eggs; serial sections showed the epi-

thelium of the common genital atrium to be present and of usual height. The return to usual height is complete in one half hour (the shortest period at which the experimental worms were checked) but may be achieved much quicker. In fact, it seems likely that the epithelial cells expand just as the pressure is removed from them but there has been no opportunity to observe this.

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A Systematic Study of the Main Arteries in the Region of the Heart—Aves XIII.

Ciconiiformes, Part I¹

Fred H. Glenny²

INTRODUCTION

During the middle and latter part of the 19th century, considerable interest was shown in the arrangement of the carotid arteries in birds (1, 3, 4, 6, 7, 8, 9, 10, 33, 35, 38, 39, 40, & 41), although in the earlier part of the century a few other workers had already laid the ground-work for such investigations (2, 32, 36, & 37). Even with this rather impressive number of workers, only incomplete information on the arterial arrangements of birds was readily available and, as a result, both incomplete and somewhat confused. More recent studies by Bhaduri (5) and Glenny (11-31) have added somewhat to our present, though still limited, knowledge of the arrangement of bird arteries. Fortunately more recent observations (11, 19, 21, 22, 25, 27, 31, & 34) give some heretofore little-known information with regard to the functional modification of certain embryonic vessels.

As Garrod (9) has already shown, members of the Ciconiiformes may be "aves bicarotidinae normales" or "aves conjuncto-carotidinae". He likewise pointed out that both *Phoenicopterus antiquorum* and *Phoenicopterus ruber* present a slight variation of the condition "aves conjuncto-carotidinae" in that the right carotid is much larger than the left just before these two vessels fuse to form a single internal carotid (trunk) artery which then enters the hypapophyseal canal of the neck.

Similarly, Garrod and others reported several other arrangements in different species and orders of birds (3). Of these, the condition "aves laevo-carotidinae", which is found in the Passeriformes (9 & 17), Piciformes (9 & 19), Trogoniformes (9 & 20), Coraciiformes (9 & 22), Trochilidae & Cypselidae, *Cacatua galerita* & *Cacatua cristata*, Turnicidae & Megapodidae, *Podiceps cristatus*, *Podiceps minor*, and *Arctica alle* (9); *Podilymbus podiceps*, *Colymbus auritus*, and *Colymbus grisegena holböllii* (Glenny, in preparation); *Rhea americana* (9, 6, & 21), *Casuarus australis* (18), and the Kiwis (*Apteryx australis* and *Apteryx owenii*) (9, 16, & 39) is one of the commonest conditions found in birds.

Of the Ciconiiformes, *Ardea cinerea*, *A. goliath*, *A. purpurea*, *A. alba*, *A. egretta*, *A. garzetta*, *A. candidissima*, and *A. herodias herodias*; *Ciconia nigra*, *C. alba*, and *Leptoptilus crumeniferus*; and *Ibis rubra*, *I. melanoccephala*,

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I. strictipennis, *I. nippon*, and *Platalea leucorodia* are reported to be bicarotidinae normales. *Botaurus stellaris*, *B. lentiginosus*, *Butorides v. virescens*, *Phenicopter antequorum* and *P. ruber* are conjuncto-carotidinae. As has already been noted, the latter two species exhibit the joined carotids—the left conjoining vessel being greatly reduced in size.

MATERIALS

Three species of the Ciconiiformes were made available for this study by Professor Tsen-Hwang Shaw, of the Fan Memorial Institute of Biology, Peiping, China, and by Dr. Alexander Wetmore and Dr. Herbert Friedmann, of the United States National Museum.

Only single specimens of *Plegadis guarauna* (Linnaeus) No. 85264, *Phenicopter ruber* Linnaeus No. 20731, and *Ixobrychus sinensis* (Gmelin) were dissected.

OBSERVATIONS

Plegadis guarauna (Fig. 1).—The innominate artery (2) divides to form the subclavian (9) and common carotid (8) arteries. The coracoid major (10), axillary (11), intercostal (12), and two pectoral (13) arteries arise in order from the subclavian artery. The common carotid gives rise to the vertebral (14), superficial cervical (17), and internal carotid (trunk) (18) arteries. The ductus shawi (16), which sends off the syringo-tracheal arteries (15), arises near the base of the vertebral artery. The thyroid artery (24) arises from the normal superficial cervical arteries. In addition to the normal superficial cervicals (17), accessory superficial cervical arteries arise from the internal carotid (trunk) arteries: the right vessel (20) divides to form two vessels which serve the oesophagus and other tissues on the right side of the neck, while the left vessel (21), which is likewise somewhat more ventrally situated, furnishes the blood supply to the cervical lymph glands and connective tissues on the left side of the neck. Both the ligamentum aortae (5) and the ligamentum botalli (6) are present and maintain their proximal connections to the pulmonary arteries (7).

Phenicopter ruber (juvenile specimen) (Fig. 2).—The branches of the subclavian artery are the same as in *Plegadis* and *Ixobrychus* except that the intercostal (12) divides into lateral and ventral branches. The common carotid (8) gives rise to the ductus shawi (16) which, as in *Plegadis* and *Ixobrychus*, gives rise to the syringo-tracheal arteries (15), and then the thyroid artery (24) before further dividing to form the vertebral (14), superficial cervical (17), and internal carotid (trunk) (18) arteries. The scapular artery (19) was found to arise as a branch of the left superficial cervical. The left internal carotid (trunk) is very small in diameter and fuses with the larger right internal carotid (trunk) before the resulting artery of fusion enters the hypapophyseal canal as a common internal carotid trunk artery. Both the ligamentum aortae (5) and the ligamentum botalli (6) are present and attached to the pulmonary arteries. No other cervical arteries were observed, although others may be present in the adult. (This specimen had been preserved in alcohol for several years before the writer examined it and this

presented certain difficulties not encountered in fresh materials.) It should be remarked here that the right superficial cervical artery serves as the ascending oesophageal artery of this species.

Ixobrychus sinensis (juvenile specimen) (Fig. 3).—Branches of the subclavian artery are the same as in *Plegadis*. The common carotid gives rise to the ductus shawi (16) before giving rise to the vertebral (14), superficial cervical (17), and internal carotid (trunk) (18) arteries. The right internal carotid alone remains as a functional vessel carrying blood to the head along the hypapophysial canal. The left internal carotid—if present—does not enter the hypapophysial canal, but remains as a superficial cervical vessel, and is greatly reduced in size. [The writer, however, feels from the present evidences that this vessel is entirely lacking and is, therefore, similar to the condition found in two species of *Eupodotis* (Garrod, 1873).] This condition would be known as "aves dextro-carotidinae" as contrasted with "aves laevo-carotidinae" of Garrod (9). The right superficial cervical artery (17) gives rise to two ascending oesophageal arteries (20) and a third vessel which serves the cervical lymph glands, connective tissues, and muscles on the right side of the neck. The left superficial cervical artery (17) supplies the cervical lymph glands, connective tissues and muscles of the left side of the neck, and also sends off a scapular branch (19). Two small vessels, the ascending tracheal arteries (23) arise from the common carotids or one of the branches of the common carotids. In addition to the ascending tracheal (23), vertebral (14), and normal superficial cervical (17) arteries, the left common carotid gives rise to a small cervical vessel (22) which serves various tissues on the left side of the neck, but is more ventral than is the normal superficial cervical artery (17). This left accessory cervical artery (22) may be homologous with the left accessory superficial cervical artery (21) of *Plegadis*. On the other hand, it may prove to be the left internal carotid artery—lying superficially as in a few other birds (9)—which may have become functionally modified through anastomoses with other vessels. The writer—at present, in lieu of adequate evidences to the contrary—feels that this vessel is probably not the left internal carotid artery of other birds, but is most probably an accessory superficial cervical artery. — To substantiate or to disprove this view, further and extensive gross anatomical, as well as embryological, studies should be carried out on this species. — The ligamentum aortae (5) is present and complete, while the ligamentum botalli (6) is present but incomplete and is partially fused with the right radix aortae (4).

DISCUSSION

The trend from the condition "aves bicarotidinae normales" to the condition "aves dextro-carotidinae" is readily observable in three distinct steps: 1) the anastomosis of left and right internal carotid (trunk) arteries resulting in the condition "aves conjuncto-carotidinae" found in *Botaurus* et al. to 2) a reduction of the left internal carotid (trunk) as in *Phoenicopterus*, and finally to 3) the complete degeneration or atrophy of the proximal portion of the left internal carotid artery as exhibited in *Ixobrychus*. A somewhat similar observation was noted by the writer in the case of *Lophoceros*

melanoleucos alboterminatus (22). In the latter case, the right vessel degenerated and became functionally modified to supply a very limited amount of blood to the ventral cervical muscles just posterior to the basal opening of the hypapophysial canal. No intermediate condition similar to that found in *Cacatua sulphurea* (9) could be found in any other closely related species.

It might be concluded—from the differences in the internal carotid (trunk) arteries, in the Ciconiiformes—that this order of birds might well be in a state of developmental flux and as a result undergoing considerable divergence in its ordinal evolution. At the present time, however, family characteristics, based upon the arrangement of the internal carotid arteries, cannot be satisfactorily established. The basic ordinal arrangement of arteries arising from the subclavian artery is characteristic and does not, therefore, point toward radical changes in the ordinal characteristics.

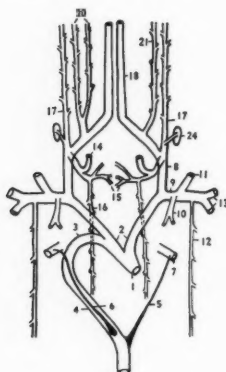


Fig. 1

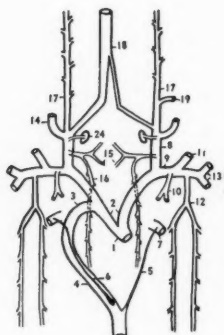


Fig. 2

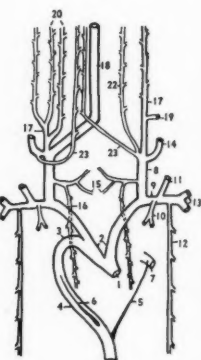


Fig. 3

Fig. 1. Ventral view of main arteries in the neck and thorax of *Plegadis guarauna*.

Fig. 2. Ventral view of main arteries in the neck and thorax of *Phoenicopterus ruber*. (Juvenile specimen)

Fig. 3. Ventral view of main arteries in the neck and thorax of *Ixobrychus sinensis*. (Juvenile specimen)

KEY TO ABBREVIATIONS

1. aortic root; 2. innominate arteries; 3. right systemic arch (4th aortic); 4. right radix aortae; 5. ligamentum aortae; 6. right ligamentum botalli; 7. pulmonary artery; 8. common carotid artery; 9. subclavian artery; 10. coracoid major artery; 11. axillary artery; 12. intercostal artery; 13. pectoral arteries; 14. vertebral artery; 15. syringotracheal artery; 16. ductus shawi; 17. (normal) superficial cervical artery; 18. internal carotid (trunk) artery; 19. scapular artery; 20. ascending oesophageal arteries (right accessory superficial cervicals); 21. left accessory superficial cervical artery; 22. (artery of uncertain origin and function)—left accessory superficial cervical artery; 23. ascending tracheal arteries; 24. thyroid artery.

The probable answer to the wide differences in the arteries of the neck and thorax, especially with regard to the anastomosis of the internal carotid (trunk) arteries may be found through embryological studies. These differences may occur as a result of the relative positions assumed by the arteries during embryonic development—especially during the period of extreme cervical elongation. It should be kept in mind that the neck of most of the Ciconiiformes is relatively longer than that of most other species of birds, and this may have some bearing on the basi-cervical anastomosis of the carotids—with the possible functional modification of other cervical vessels of the adult.

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Catch of *Stizostedion vitreum* in Relation to Changes in Lake Level in Western Lake Erie During the Winter of 1943¹

Kenneth H. Doan

INTRODUCTION

About the island archipelago in western Lake Erie there is a hook and line fishery through the ice. Fishermen are able to operate for about two months during most seasons, and in recent years have shipped to market an average of nearly 50,000 pounds of fish each winter.

A season's total catch depends upon the nature and extent of the ice cover, which governs the length of the fishing season, upon the number of fishermen, and upon the availability of fish. The latter is in part dependent upon the absolute number of fish present upon the grounds, and in part upon factors which modify contacts between fish and fishermen, such as water current. The present paper offers the results of a measure of the catch, and the probable nature of changes in catch owing to fluctuations in lake level.

CATCH

The winter fishery, where the following observations were made, centers upon Put-In-Bay on South Bass Island, Ottawa County, Ohio. Fishing is done from small, coal-heated shanties which one man can easily move on runners from place to place. Through a rectangular hole in the shanty floor and ice the fisherman lowers two lines, each weighted with a flat lead sinker and bearing a spreader and two hooks. The lake shiner, *Notropis a. atherinoides* Raf., is used for bait. The principal fish caught is the yellow pikeperch, *Stizostedion v. vitreum* (Mitch.), locally called pickerel. The remainder of the catch consists of sauger *S. c. canadense* (Smith), yellow perch *Perca flavescens* (Mitch.), and a few blue pike *S. v. glaucum* Hubbs. Additional description of this fishery may be found elsewhere.²

Fish buyers have submitted reports of the poundages purchased by them each season, according to species and month. The total catch sent to market in 1943 amounted to 60,336 pounds. Fish caught and taken home by visiting sportsmen, and fish smaller than commercial grades (minima: pickerel 13 inches, perch 8½ inches, sauger and blue pike 11 inches) and consumed by the fishermen probably did not exceed 20 per cent, or 6 tons.

¹ This investigation was carried out at the Ohio State University's Franz Theodore Stone Laboratory, on Lake Erie, and some assistance was received from the Ohio Division of Conservation and Natural Resources.

² See Doan, K. H. 1943—Ice fishing as a community pursuit in the Lake Erie islands. Ohio Conserv. Bull. January 1938 pp. 19-20, and The winter fishery in western Lake Erie, with a census of the 1942 catch. Ohio Jour. Sci. 44(2):69-74.

One buyer, who purchased 50 per cent of the total marketed catch, furnished originals of sales slips issued to every fisherman at each transaction.

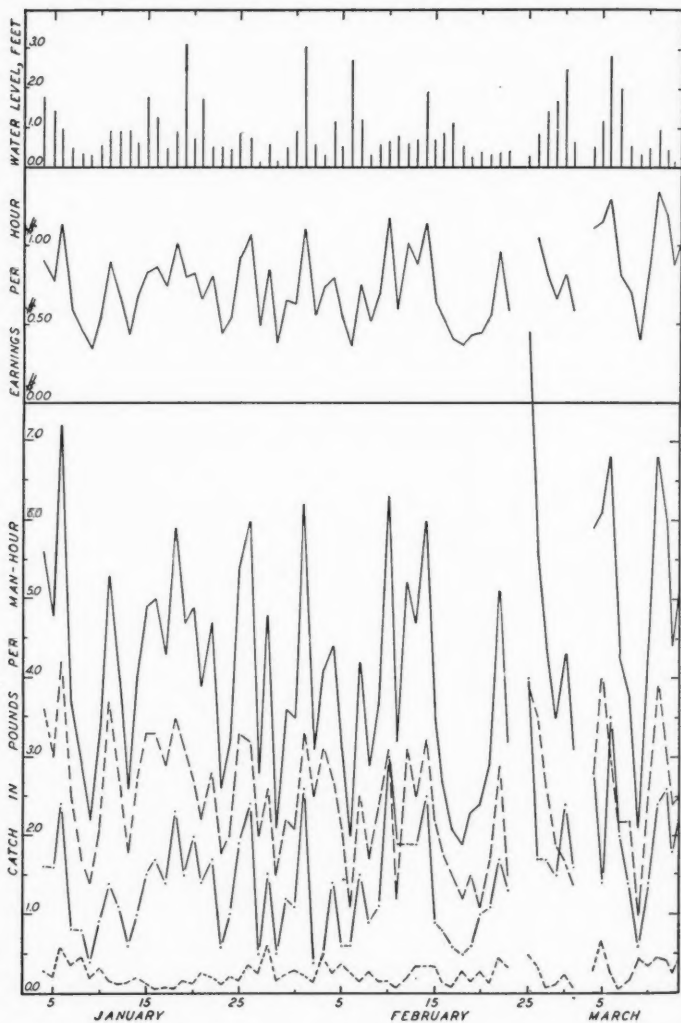


Fig. 1. Graph showing daily changes in water level, fishermen's earnings, and catch in the winter fishery at Put-In-Bay, Ohio. ————— all species, — — — — No. 2 pickerel, — — No. 1 pickerel, perch and sauger.

These slips showed the poundages of each species, price paid, and the number of hours fished, and have served as creel census cards. The daily average catches in pounds per man-hour are illustrated in Fig. 1, and semi-monthly average catches are presented in Table 1.

TABLE 1.—Average catches by ice fishermen in Lake Erie at Put-In-Bay, 1943.

Period	No. of census reports	Average length of fishing day, hours	Fish caught, pounds per man-hour					Earnings per man-hour
			Pickerel			Perch and sauger ⁵	Total fish	
			No. 13	No. 24	Total			
Jan. 3-15	233	7.13	1.11	2.63	3.74	0.29	4.03	\$0.66
Jan. 16-31	265	8.27	1.51	2.69	4.20	0.19	4.39	0.75
Feb. 1-15	155	8.45	1.52	2.41	3.93	0.25	4.18	0.77
Feb. 16-28	99	8.00	1.56	2.25	3.81	0.25	4.06	0.77
Mar. 1-15	129	8.33	1.99	2.77	4.76	0.32	5.08	0.99
Season	881	7.98	1.50	2.59	4.09	0.25	4.34	0.77

³ Pickerel over 1 pound.

⁴ Pickerel between 13 inches (about $\frac{3}{4}$ pound) and 1 pound.

⁵ Perch and sauger were unfortunately grouped together because they were taken in small quantity in 1943, and were the same price. Observations indicated them to be about equally divided by weight. Blue pike infrequent, and included here also.

There was no marked trend in success of fishing through the 1943 season, with the exception of better fishing for larger pickerel in the latter part of the winter. This is perhaps explained on the assumption that more large fish moved towards the breeding grounds in this vicinity as the time for spawning approached. Increased average earnings, in spite of a slight decrease in rate of catch, reflected increases in the price of fish.

LAKE LEVEL

In most winters the islands in western Lake Erie are joined together by a bridge of ice. Eastwards the ice is not continuous, and sometimes there is open water to the north and west. Beneath the ice in the island region the water flows with varying intensities of current, and for various periods of time. The natural ebb and flow of small currents are more noticeable and affect the success of fishing.

Many observations of the currents on the fishing grounds in 1943, made by noting the slant and vibrations of fish lines, were recorded under the more or less subjective headings of "none", "slight", "strong", etc. The desire to translate these rough observations into terms of some precision led to an investigation of the relationship between change in water level and the strength of the current. Lake surface level is under continuous measure by a Friez gauge operated by this laboratory at Put-In-Bay for the War Department's United States Lake Survey Office. This machine transcribes on a rotating drum an ink line which records the changing positions of a float supported at surface level.

Although currents during the night may change the abundance of fish in a given area, only those currents in action during the normal fishing day were compared with lake levels. This is included in the period 8:00 to 20:00 hours (8:00 A.M. to 8:00 P.M.). Classifications of observed currents were compared with the sum of water level changes by half-day periods. It may be seen

TABLE 2.—Observed relative currents and corresponding water level changes in hundredths of feet, in Lak Erie at Put-In-Bay during the winter of 1943. Each observation refers to the period between 8:00 and 12:00 hours or 14:00 and 18:00 hours, so as to take advantage of current observations made in morning or afternoon only.

	Observed current				
	none	light	moderate	strong	very strong
Mean water level change	10	17	27	54	90
Standard error of mean	7	7	12	25	54
Number of observations	8	13	13	8	5

(Table 2) that currents designated from "none" to "very strong" were accompanied by water level changes from 0.10 to 0.90 feet, respectively. The trend is distinct enough to warrant the use of measures of change in water level in the absence of absolute measures of current.

CATCH, AND VARIATIONS IN LAKE LEVEL

The rate of catch of pickerel fluctuated from day to day during the winter, as was seen in Fig. 1. Experience indicated that better fishing was often promoted by stronger currents, so that an investigation of the relationship between them seemed in order.

Sixty-seven pairs of observations on rate of catch of pickerel and amount of change in lake level were available (Fig. 1). Division of the observations into six groups served to indicate the general shape of the curve, and to determine that an equation of the type

$$Y = a + b \log X$$

would be applicable. The curve was divisible into two separate parts, the X_1 or lake level, value of 0.88 feet serving as the point of separation. The shape of the line representing the relationship between catch and changes in water level was curvilinear, and prompted the use of regression methods rather than simple linear correlation.

Calculation of regression coefficients for the first part of the curve showed that the relationship could be stated in the form

$$Y = 0.15 + 2.08 \log X$$

where Y represents the catch of pickerel in pounds per man-hour, and X represents the sum of changes in water level between 8:00 and 20:00 hours in hundredths of feet. The standard error of estimate is 1.06. Consideration of the ratio of the standard error of the regression coefficient to the coefficient itself indicates a probability of about 0.01 which is highly significant. Similar treatment of the second part of the curve (X_2 , from 89 to 318 hundredths

feet) yielded the information that variations were too large to allow of significance.

DISCUSSION AND CONCLUSIONS

A measure has been obtained of the availability of fish by ice fishing in western Lake Erie during the winter of 1943. That this measure may be high owing to the absence of reports of zero catches is conceded, but unreported poundages of small fish taken from the lake probably balance this in part. The absolute numbers of fish present on the fishing grounds is likely the most important factor in determining the general level of the rate of catch.

However, daily modifications in the rate of catch of pickerel are attributed mostly to changes in intensities of the water currents, as measured by changes in lake level. Preliminary tests of the effect upon rate of catch have been made for daily solar radiation, wind velocity, and turbidity of the water. While correlations are high in a number of instances between catch and these other factors, only currents, as measured by changes in water level, seem to offer a consistent explanation of daily variations in average catch throughout the winter.

It is suggested that changes in intensity of current probably cause pickerel to move—to swim into the current, to drop back, to seek protection near the bottom. When increased currents activate the pickerel, then in their movements the fish increase their chances of seeing and swallowing a baited hook, and heavier catches are made.

It is realized that in this problem the relationship between catch and current could be made more precise by employing actual continuous measurements of current. But, in the absence of such measures, it would seem that water level changes serve satisfactorily even though indirectly.

SUMMARY

From Jan. 3 to March 15, 1943, fishermen caught and marketed 60,336 pounds of fish taken by hook and line in western Lake Erie in the vicinity of Put-In-Bay, Ohio.

A measure of the season's catch employed the use of 881 sales slips as creel census cards, and showed that pickerel were taken at an average rate of 4.09 and perch and sauger at a rate of 0.25 pounds per man-hour, or a total catch at the rate of 4.34 pounds per man-hour, worth \$0.77 per hour to the average fisherman.

Average success in fishing did not fluctuate widely with the exception of heavier catches of large pickerel in March.

It was shown that measures of variation in the rate of flow of water under the ice could be obtained indirectly by employing continuous records from a gauge which measured fluctuations in lake level.

Between daily water level changes of 0.00 and 0.88 feet, the relation between pickerel catch in pounds per man-hour, Y , and changes in water level in hundredths of feet, X , was

$$Y = 0.15 + 2.08 \log X$$

Above 0.88 feet variations were too extreme to permit of significant results.

Currents probably affect the movements of pickerel, and hence their chances of contact with a fisherman's baited hook.

Studies in *Phacelia*—Revision of Species Related to *P. Douglasii*, *P. linearis*, and *P. Pringlei*

John Thomas Howell

Introduction

The species of *Phacelia* reviewed in this paper belong to the section *Eutoca* and may be distinguished from other species in that strictly North American group by their annual or rarely biennial habit, deciduous and usually open or rotate-campanulate corollas, deeply parted or divided style, and usually acute and ovate capsule. The group is predominantly Californian with only four of the twenty species extra-Californian and with thirteen endemic to the state. The species may be divided into three rather easily separable groups: those related to *P. Douglasii* marked by elongate pedicels, those related to *P. linearis* marked by short pedicels and subequal calyx-divisions, and those related to *P. Pringlei* marked by strongly unequal calyx-divisions and usually short pedicels. The species are closely related for the most part, and because of the fluctuating variations in some of the characters, the entities are sometimes difficult to separate even by means of highly critical criteria. With the use of new criteria, however, and with a shift of emphasis in the application of several old criteria, a new alignment of species is suggested, which, I believe, is more natural from the viewpoint of probable phylogeny and which will make easier and more certain the identification of the species.

Two distinct kinds of species occur in the group: the relatively unvarying type with localized or markedly disjunct distribution, and the usually more common and variable species with wider-ranging distribution. Of the former type, *P. Pringlei* Gray, which apparently is restricted to a single mountain ridge in northwestern California, is an excellent example; and the rather widespread and variable *P. Douglasii* (Benth.) Gray of central and southern California is an example of the second type. Because of the rather wide distribution of these frequently narrow endemics from California to the mountains north of the Great Basin, and because of the frequently close morphologic interrelation of the widely separated species, it is believed that these entities are remnants or relicts of a variable complex that was generally distributed in western North America in the late Tertiary preceding the Pleistocene orogeny and glaciation. From my study of the present-day species-groups, it seems probable that differentiation had progressed quite far in the complex as a whole before the Pleistocene revolution and the subsequent or concurrent glaciation; but it also seems quite evident that in some instances (as in the case of *P. Pringlei* and its immediate relatives), divergence along specific lines has been relatively recent and has been promoted by the high degree of isolation resulting from the topographic and climatic changes.

The view that the phylogenetic development of the present-day entities as well as their occurrence has been intimately connected with the geologic history

of western North America has definitely influenced my interpretation of species, which, it may be noted, is not conservative. In a truly conservative view of this group, the number of species would be about a third less; but from the viewpoint of probable descent, I can see no advantage in treating a given entity in a subspecific category when it is morphologically distinct and is geographically isolated as the result of orogenic activity. Any conservative botanist viewing the case objectively would conclude perforce that *P. Purpusii* T. S. Brandg. and *P. grisea* Gray are only varietally distinct; but when the small but definite structural differences between the two are viewed from the viewpoint of history and geography, the differences in my estimate call for specific recognition of both entities. On the other hand, in more variable and widespread species the taxonomic recognition of minor variations has been reduced to a minimum, only two varieties among all the species being recognized. In several of the species there are notable variations but as a rule the differences within the species are too nearly confluent or are entirely unrelated to geographic or ecologic distribution to be given nominal recognition. Thus, while the large-flowered form of *P. Davidsonii* Gray is very different from the typical aspect of the species, the line of division would have to be entirely arbitrary; and while some forms of *P. Douglasii* are rather distinctive, they not only merge with the general character of the species but show not the least distributional or ecological segregation which might lend emphasis to a small structural difference. Hence *P. Davidsonii* Gray and *P. Davidsonii* var. *macrantha* Parish are not distinguished, although it is conceivable that they would be accepted as two species if only the strictly typical forms of the two survived some geologic revolution. In contrast are *P. grisea* and *P. Purpusii* which are actually but little more distinct than the more diverse elements in *P. Davidsonii*, but which are accepted as species because the stability of their structural differences indicates entities which have been geographically isolated for a longer or shorter period of geologic time.

Acknowledgments.—The present revision is based chiefly on the collections in the Herbarium of the California Academy of Sciences (CAS), many of the specimens having been given to me by friends over a period of years now approaching two decades. For all of these I am very grateful. Also I have had the privilege of studying collections deposited in many institutions and to the curators of these herbaria I am grateful for their generous cooperation. These institutions, together with the symbols used in citing collections from them, are as follows:

- Dudley Herbarium, Stanford University (DS);
- Field Museum (F);
- Frank W. Peirson (FP);
- Gray Herbarium, Harvard University (G);
- Greene Herbarium, Notre Dame University (ND);
- Missouri Botanical Garden (M);
- New York Botanical Garden (NY);
- Pomona College (P);
- Rancho Santa Ana Botanical Garden (RSA);

University of California (UC);
 United States National Herbarium (US);
 Willamette University (W);
 Washington State College (WS).

KEY TO THE SPECIES

1. Lower pedicels much longer than the upper, the lower frequently as long as, or longer than, the fruiting calyces and generally sigmoid-spreading or recurved. (See also *P. oregones* and *P. minutissima*, the former subalpine in the Sierra Nevada of California, the latter in the mountains north of the Great Basin.)
2. Capsule turgid at least below the middle, ovate, generally acute and attenuate into a prominent beak; corolla-scales attached to corolla along one side (except sometimes in *P. stellaris* in which the corollas are only 3-5 mm. long and the filaments are glabrous), or rarely corolla-scales obsolete.
3. Ovules 6-17; seeds 1-2 mm. long; leaves entire or pinnately lobed or divided, the lobes usually pointing forward, the terminal lobe with lateral veins; filaments long-hairy at the middle.
4. Leaves mostly entire; corolla 4-6 mm. long; style and branches 2-3 mm. long 1. *P. curvipes*
4. Leaves entire or lobed; corolla mostly 7-15 mm. long; style and branches 4-7 mm. long 2. *P. Davidsonii*
3. Ovules 20-60; seeds mostly 0.5-1 mm. long; leaves once or twice pinnately divided or lobed (or very rarely entire in *P. Douglasii* var. *petrophila* in which the filaments are glabrous), the lobes of the leaves generally divaricately spreading and the terminal lobe generally without lateral veins.
5. Corolla 6-13 mm. long; stamens 3-6 mm. long, the filaments hairy or glabrous; style and branches 2-6 mm. long 3. *P. Douglasii*
5. Corolla 3-5 mm. long; stamens 2 mm. long, the filaments glabrous; style and branches 1-2 mm. long 4. *P. stellaris*
2. Capsule compressed, obovate, obtuse; corolla-scales free from corolla along lateral margins; filaments glandular-puberulent; corolla 6-11 mm. long; seeds 1-2 mm. long 5. *P. insularis*
1. Pedicels short, the lower not much longer than the upper and generally straight, or if elongate (as in *P. oregones*, *P. minutissima*, and *P. vallicola*) the fruiting sepals markedly unequal in length.
6. Calyx-divisions in fruit nearly equal; corollas mostly 7-16 mm. long; filaments long-hairy or more or less glandular (smooth or only tuberculate in *P. Congdonii* and sometimes glabrous in *P. Franklinii*); style-branches usually shorter than the undivided part of the style (or sometimes longer in *P. phacelioides*).
7. Capsules more or less compressed, the valves with prominent raised cord-like midrib (evident only near base of valves in *P. phacelioides*); anthers 0.25-0.75 mm. long; leaves generally entire, elliptic to ovate.
8. Corolla open-campanulate to rotate-campanulate; stamens 3-11 mm. long; style and branches 4-10 mm. long; ovules 9-20.
9. Stamens 6-11 mm. long, the filaments glandular-tuberculate and usually long-hairy; style and branches 6-10 mm. long; corolla-scales 2.5-4 mm. long 6. *P. divaricata*
9. Stamens 3-5 mm. long, filaments smooth or tuberculate, not long-hairy; style and branches 4-5 mm. long; corolla-scales 1-2.5 mm. long 7. *P. Congdonii*
8. Corolla tubular-campanulate; stamens 2-2.5 mm. long; style and branches 2 mm. long; ovules 8 8. *P. phacelioides*
7. Capsules turgid, the valves without a prominent cord-like midrib; anthers 1-1.3 mm. long; leaves generally lobed or divided (if entire, then linear or oblong-linear).
10. Leaves entire or divided, linear to narrowly oblong if entire, the divisions narrow if divided; corolla-scales between filaments connate; seeds coarsely pitted, the pits not aligned longitudinally 9. *P. linearis*

10. Leaves pinnately parted, the segments oblong to deltoid; corolla-scales between filaments not connate; seeds finely pitted, the pits tending to be aligned longitudinally 10. *P. Franklinii*
6. Calyx-divisions in fruit more or less unequal, especially in the lowest flowers; corollas 2-7 mm. long; style divided to below the middle (except sometimes in *P. minutissima*).
11. Corolla-tube without definite translucent areas behind the stamens; corollas 2-6 mm. long; stamens 1.5-6.5 mm. long; style and branches 1-6 mm. long.
12. Leaves linear to lanceolate or oblanceolate (except in *P. verna*); ovules 4-12; capsule acute to obtuse, short-beaked, back of valves more or less prominently longitudinally sulcate.
13. Leaves ovate-lanceolate to ovate; corolla sparsely long-hairy on veins inside; filaments smooth and glabrous 11. *P. verna*
13. Leaves linear to lanceolate or oblanceolate; corolla glabrous inside; filaments smooth, tuberculate-roughened, or hairy.
14. Stamens 3-5 mm. long; style and branches 3.5-5 mm. long.
15. Lower pedicels not elongate.
16. Corolla 5-6 mm. long; stamens 5 mm. long, the filaments hairy; ovules 8-11 12. *P. Peckii*
16. Corolla 3-4 mm. long; stamens 3-3.5 mm. long, the filaments roughened; ovules 4-7 13. *P. Pringlei*
15. Lower pedicels elongate and generally sigmoid-divaricate 14. *P. oregenes*
14. Stamens 1.5-2 mm. long; style and branches 1-2 mm. long.
17. Style and branches 2 mm. long; ovules 6-8; capsule 3-3.5 mm. long 15. *P. Leonis*
17. Style and branches 1 mm. long; ovules 11 or 12; capsule 5 mm. long 16. *P. minutissima*
12. Leaves elliptic to ovate; ovules 18-25; capsule acuminate into a long beak; back of valves with an impressed longitudinal line 17. *P. vallicola*
11. Corolla-tube with definite translucent areas behind each stamen; corollas 5-7 mm. long; stamens 5-8 mm. long; style and branches 5-9 mm. long.
18. Leaves narrowly oblong to ovate, lateral veins prominent, impressed above and raised below; fruiting sepals narrowly oblong-spatulate to broadly obovate-spatulate, mostly obtuse.
19. Stems glandular-puberulent or glandular-hirsutulous; ovules 4-8 18. *P. Purpusii*
19. Stems glandular-hirsute; ovules 10-12 19. *P. grisea*
18. Leaves usually linear or narrowly oblong, lateral veins not prominent or lacking; fruiting sepals linear to narrowly oblong-spatulate, mostly subacute or acute 20. *P. mohavensis*

Taxonomic Treatment

1. PHACELIA CURVIPES Torr. in Wats. Bot. U. S. Geol. Explor. 40th Paral. (King's Exped.) 252 (1871)

P. curvipes Torr. var. *eu-curvipes* Brand, Univ. Calif. Publ. Bot. 4:222 (1912).

Root annual; stems erect or somewhat spreading, few-branched at or near the base, 3-15 cm. tall, hirsute and hirsutulous, the hairs on the stems not glandular, the inflorescence with scattered capitate glands; leaves linear-oblong or linear-oblanceolate to elliptic, 1-4 cm. long, 0.2-1.2 cm. wide, with longer and shorter subappressed non-glandular hairs, entire or very rarely with a shallow lobe near the base, acute or obtuse, at base cuneate-attenuate into a narrowly bordered petiole, petiole to 2 cm. long; racemes laxly flowered below, densely

flowered above, pedicels more or less curved, the lowest to 3 cm. long, the uppermost much shorter and sometimes only 1 mm. long; calyx-divisions in flower 3-7 mm. long, 0.5-1 mm. wide, in fruit becoming 6.5-10 mm. long and 1-2 mm. wide, about equal in length but somewhat unequal in width, linear-oblong to oblong, hirsute and puberulent, not glandular or sparsely so; corolla lavender to pale violet, campanulate, 4-6 mm. long, tube 3-3.5 mm. long, whitish; corolla-scales 1-1.5 mm. long, broadly linear or oblong, truncate or attenuate at apex, the adjacent scales between filaments generally free, sometimes connate throughout; stamens 2.5-3 mm. long, filaments long-hairy at the middle, anthers 0.3 mm. long, style and branches 2-3 mm. long, the branches 1-1.25 mm. long, the style long-hairy near base; ovary 0.7 mm. long, long-hairy, ovules 6-17; capsule 4 mm. long, deltoid-ovate, compressed especially above, acute and prominently beaked, hirsute and puberulent, not glandular, the back of the valves with slightly impressed line but not sulcate; seeds about 1 mm. long, ovate, coarsely pitted, brown.

Slopes of mountains in or bordering the desert from central Nevada to southern California and southwestern Utah, 4000 to 8000 ft.

Although the morphologic characters that have been marshalled for the specific separation of *P. curvipes* and *P. Davidsonii* are neither too strong nor too exclusive, they are believed to be quite sufficient when *P. curvipes* is properly appreciated as a widespread and almost unvarying entity. To combine the two species as was done by Brand (1913, p. 115) effects a taxonomic chimera in which must be recognized perforce the two entities I choose to distinguish specifically. The very genetic make-up of the two entities argues their separation as species, the one so constant, the other so variable; and this consideration, supported by a combination of several small differences in habit, foliage, and flower, as well as an essentially different geographic distribution, is indicative, I believe, of two natural but very closely related species. In *P. curvipes* the erect stems are generally 10 cm. or less tall, the leaves are almost always entire, the corollas are 6 mm. or less long, the corolla-scales are generally free, and the styles and branches are only 2 to 3 mm. long. Rarely the corollas in *P. Davidsonii* are only 6 mm. long but in such instances the styles are 5 mm. long; one collection of *P. Davidsonii* has been seen in which the styles are only 2 to 3 mm. long but in it the leaves are generally lobed and the corollas are large and showy.

Collections. California: Whiskey Creek at 7,000 ft., Mono Co., *J. T. Howell No. 14291* (CAS), *Noldeke in 1938* (CAS); Sierra foothills south of Bishop, Inyo Co., *Heller No. 8228* (CAS, DS, F, M); 5 miles west of Independence, Inyo Co., *Kerr No. 659* (CAS); Westgard Pass, Inyo Co., *Eastwood & Howell No. 9614* (CAS); above Wild Rose Canyon, Panamint Mts., 8000 ft. Inyo Co., *Hoffmann No. 440* (CAS); Panamint City, Panamint Mts., 7100 ft. Inyo Co., *J. T. Howell in 1928* (CAS); Cajon Pass, San Bernardino Co., *S. B. & W. F. Parish No. 1311* (DS), *Johnston in 1920* (P); top of Cushenbury Grade, San Bernardino Mts., San Bernardino Co., *Hilend No. 438* and *449* (CAS); east of Tecopa Pass, Kingstons Range, 4700 ft., San Bernardino Co., *Alexander & Kellogg No. 2338* (UC); Piñon Alta, San Bernardino Co., *Jaeger in 1939* (P); Palms to Pines Highway, Riverside Co., *Winblad in 1937* (CAS); El Toro Peak, Santa Rosa Mts., 7,000 ft., *Hall No. 1170* (DC, UC); trail from Oak Grove to Palomar Mt., San Diego Co., *Peirson No. 6709* and *8354* (CAS, FP), *Munz 10399* (P); Laguna Mt., San Diego Co., *Sanford in 1927* (CAS). Nevada: Verdi, Washoe Co., *Sonne in 1890* (UC); Steamboat Springs, Washoe Co.,

Sonne No. 535 (ND); Trinity Mts., Pershing Co., Watson (Bot. King's Exped. p. 253); Empire City, Ormsby Co., M. E. Jones No. 3984 (CAS,DS,M,P,US); near Oak Springs, Belted Range, 5600 ft., Nye Co., Ripley & Barneby No. 3455 (CAS); Mt. Magruder, Esmeralda Co., Purpus No. 5922 (P,UC,US); Mormon Mts., Lincoln Co., Kennedy & Goodding No. 89 (CAS,DS,M,UC,US); Good Springs, Clark Co., M. E. Jones in 1905 (P), K. Brandegee in 1915 (UC). Utah: Beaver Dam Mts., Washington Co., Maguire No. 20553 (CAS); Clear Creek Canyon, Washington Co., Eastwood & Howell No. 9233 (CAS); Silver Reef near Leeds, Washington Co., M. E. Jones No. 5163ab (P,US).

None of Watson's collections on which *P. curvipes* was based has been seen. These were originally given by Torrey (p. 253) as from the "foothills near Carson and Washoe Cities and on the Trinity Mountains, Western Nevada; 4,500-7,000 feet altitude."

2. PHACELIA DAVIDSONII Gray, Proc. Amer. Acad. 10:324 (1875)

- P. Davidsonii* Gray var. *macrantha* Parish, Erythea 6:90 (1898); forma robusta foliis integris vel lobatis, floribus 15 mm. longis. *P. Davidsonii* var. *grandiflora* Parish in herb.; nomen nudum ex Greene, Pittonia 5:23 (1902).
P. Aldersonii Greene, Pittonia 5:22 (1902); forma foliis integris, floribus 8 mm. longis.
P. nemophiloides Greene, Pittonia 5:23 (1902); forma robusta foliis integris, floribus 8-10 mm. longis.
P. pratensis Heller, Muhlenbergia 2:236 (1906); forma foliis integris, floribus 10-12 mm. longis.
P. curvipes Torr. var. *pratensis* (Heller) Brand, Univ. Calif. Publ. Bot. 4:222 (1912).
P. curvipes Torr. var. *Davidsonii* (Gray) Brand, Pflanzenr. IV, 251:115 (1913).
P. curvipes Torr. var. *Davidsonii* fma. *eu-Davidsonii* Brand, loc. cit.
P. curvipes Torr. var. *Davidsonii* fma. *macrantha* (Parish) Brand, ibid., p. 116.

Root annual; stems erect or laxly and widely spreading, few- to many-branched at or near the base, mostly 1-3 dm. long or shorter in depauperate specimens, sparsely to densely pilose and hirsutulous, sometimes becoming canescent, mostly non-glandular below but more or less glandular in the inflorescence; leaves variable in size and shape, linear-oblong to elliptic and narrowly ovate, entire or commonly shallowly to deeply pinnately lobed and divided, 1-8 cm. long, 0.2-3.5 cm. wide, hirsutulous and finely strigose, green or more or less canescent, not glandular, acute to obtuse, cuneate at base and somewhat decurrent along the petiole, petiole to 4 cm. long; racemes arising near the base of the plant or at the ends of branches, hirsutulous with some capitate glands or the glands sometimes lacking, flowers distant below, crowded above, the lower pedicels elongate and up to 3 cm. long, the upper much shorter; calyx-divisions in flower 4-9 mm. long, 0.5-2 mm. wide, nearly equal in length, unequal in width, in fruit the divisions 5-12 mm. long, 0.75-3 mm. wide, linear to narrowly oblanceolate, hirsute and puberulent, glandular hairs present or lacking; corolla open-campanulate to rotate-campanulate, the lobes and upper part of the throat violet or lavender and the lower part of the throat white or occasionally the entire corolla white, 7-15 mm. long, the tube 3-9 mm. long; corolla-scales 1-3 mm. long, linear or narrowly oblong, truncate or attenuate above, the free edges of adjacent scales between the filaments generally connate; stamens 2.5-8 mm. long, filaments long-hairy at the middle, anthers 0.3-0.5 mm. long; style and branches mostly 4-7 mm. long, the branches 1-3 mm. long, the style and sometimes the base of the branches with

scattered hirsutulous hairs; ovary about 1 mm. long, long-hirsute, not glandular, ovules 9-17; capsules 4.5-7 mm. long, oblong-ovate to round-ovate, usually prominently beaked, hirsutulous and puberulent, rarely glandular, the back of the valves not sulcate; seeds ovate, 1-2 mm. long, brown, coarsely pitted.

Rocky and sandy slopes and flats in the mountains, often under pines, from Storey Co., Nevada, and Inyo Co., California, south to the mountains of southern California in San Diego Co., 2000 to 8000 ft.

Although certain trends of variations in this complex species are discernible along geographic lines, no variant is here given nominal recognition because the characters are so highly variable and the limits would have to be so distinctly arbitrary. The division of the complex into a series of varieties and forms has been attempted by Brand (1913, p. 115), and the key that he presents is as inadequate as it is artificial when it is applied to a large series of specimens. It is true that in the northern range of *P. Davidsonii* the leaves are mostly entire, but occasionally throughout its range occur other variants also with entire leaves. The size of the corolla is quite variable but the variability is frequently so great even in the plants of a small area or of a single collection that its value as an indicator seems to be more genetic than taxonomic. The great difference observed in size and vigor of plants is believed to be largely a reaction to edaphic conditions, though in some instances it is probably genetic, too.

Through the generous cooperation of the Gray Herbarium I have been able to examine the type of *P. Davidsonii* which was collected in Kern County, California, by Prof. George Davidson. It is representative of that rather considerable population found in the southern Sierra Nevada and Tehachapi district, a variant in which the corollas are smaller than they usually are in regions either to the north or to the south. In San Bernardino Mts., Parish's var. *macrantha* occasionally has corollas as much as twice as large. That Gray early modified his concept to include considerable variation is evident from the fact that 3 years after describing *P. Davidsonii* he cited with the Davidson specimen the southern Californian collection made by Parry and Lemmon in 1876 (1878, p. 167). In this the corollas are 8 to 10 mm. long and the leaves are sometimes divided, sometimes entire. He was aware of the variation thus introduced into the original concept but he believed that the type specimen of *P. Davidsonii* represented only a "depauperate and small-flowered form." In the synonymy given above I have briefly indicated to which forms the other principal and primary names in this complex are to be referred.

Brand (1913, p. 115) in his treatment of synonymy for this group displayed his lack of appreciation of relationships and identity of plants. *Phacelia Aldersonii* Greene is not a form of *P. curvipes* but of *P. Davidsonii*; *P. Congdonii* Greene is more closely related to *P. divaricata* than to any species with which we are immediately concerned; and *P. curvipes* var. *yosemitana* Brand is exactly *P. vallicola* Congdon! The oldest varietal epithet to be used for *P. Davidsonii* if it is reduced to *P. curvipes* is not *Davidsonii* as used by Brand, but *macrantha* which was published by Parish 25 years earlier.

Collections. Nevada: Virginia City, Storey Co., *K. Brandegee in 1884* (UC). California: foothills west of Bishop, Inyo Co., *Heller No. 8273* (CAS, type of *P. pratensis*; M, UC); Kern County, *Davidson* (G, type of *P. Davidsonii*); Greenhorn Range, Kern Co., *J. T. Howell No. 5075* (CAS,F,G,ND,NY,P, RSA), *Hall & Babcock No. 5054* (DS,UC); Tehachapi, Kern Co., *Greene in 1889* (ND); Mt. Pinos, Ventura Co., *Munz No. 6963* (P,UC), *J. T. Howell No. 3842* (CAS,F,G,M,ND, NY,US,W,WS); Topatopa Mts., Ventura Co., *Abrams & McGregor No. 100* (DS, US, corolla 4-5 mm. long), *No. 101* (DS, corollas 6-8 mm. long), *No. 102* (DS,US, corollas 8-11 mm. long); upper Sespe Creek, Ventura Co., *Munz No. 13235* (P); Big Pine, San Rafael Mts., Santa Barbara Co., *Hoffmann in 1929* (CAS); southern California, *Parry & Lemmon No. 259* (CAS,F,G,M,UC,US); Tejon Pass, Los Angeles Co., *Pringle in 1882* (CAS,F,US); summit of Mt. Wilson, San Gabriel Mts., Los Angeles Co., *G. B. Grant No. 6886* (CAS,DS,P); Arrastre Canyon at 4500 ft., San Gabriel Mts., Los Angeles County, *Ewan No. 7210* (CAS,ND); Lytle Creek Canyon at 6000 ft., San Gabriel Mts., *H. M. Hall No. 1431* (CAS,DS,UC); south slope of San Bernardino Mts., 4000-6000 ft., San Bernardino Co., *Parish No. 3771* (ND, type of *P. nemophiloides*; UC,US); near Lake Arrowhead, San Bernardino Mts., San Bernardino Co., *Hilend No. 210* (CAS); South Fork Santa Ana River, 6200 ft., San Bernardino Mts., San Bernardino Co., *J. & H. W. Grinnell No. 245* (CAS,US); Santiago Peak, Santa Ana Mts., Orange and Riverside counties, *Abrams No. 1836* (DS,P); San Diego Co., *Vasey No. 417* (CAS,F,ND); Witch Creek, San Diego Co., *Alderson No. 21* (ND, type of *P. Aldersonii* Greene; US); Laguna Mts., San Diego Co., *Munz No. 9664* (P).

Occasionally where the western range of *P. curvipes* touches or overlaps the range of *P. Davidsonii* perplexing intermediates occur which may have arisen through hybridization. These are common in the San Bernardino Mts., especially in Bear Valley and vicinity, and the following may be cited as representing this intermediate: Bear Valley, *M. E. Jones in 1900* (P), *Harwood No. 4334* (P), *J. T. Howell No. 2728* (CAS,F, NY, RSA); 2 miles east of Bluff Lake, *Munz No. 5623* (P,UC). These collections are more like *P. Davidsonii* than *P. curvipes*; elsewhere an occasional form resembles *P. curvipes* more closely: Big Pines, San Gabriel Mts., Los Angeles Co., *Feudge No. 1217* (P); Santa Rosa Mts., *Jaeger in 1928* (P).

3. PHACELIA DOUGLASII (Benth.) Torr. Bot. Mex. Bound. Surv. 143 (1859)

Root annual; plants diffusely branched from the base, the stems prostrate, ascending or erect, or rarely the plants simple below and branching above, 0.5-4 dm. long, hirsute and hirsutulous or even setose-hispid, sometimes canescently puberulent, more or less glandular or sometimes without glands; leaves variable, linear-oblong or oblanceolate to elliptic, very rarely entire, generally pinnately lobed or divided, the lobes or divisions fine or coarse, oblong, ovate-triangular or roundish, discreet or more or less confluent with smaller intermediate segments, the lobes entire, toothed or pinnatifid, obtuse or acute, the blades subappressed-hirsutulous to canescently puberulent or strigose, 1.5-7 cm. long, 0.5-2 cm. wide, petioles mostly 1-5 cm. long; racemes very laxly and distantly flowered below, to 3.5 dm. long, pedicels mostly 0.5-1 cm. long, the lowest sometimes much longer and uppermost shorter, hirsute and puberulent and more or less glandular, the puberulent hairs spreading, reflexed, or rarely ascending; calyx-divisions in flower 4-6 mm. long, 0.6-1 mm. wide, in fruit 7-10 mm. long, 1-3.5 mm. wide, linear-oblanceolate to oblanceolate-spatulate, about equal in length, a little unequal in width, hirsute, sometimes glandular, obtuse or subacute; corolla lavender, campanulate to broadly campanulate or subrotate, 6-13 mm. long, lobes rounded, 1-7 mm. long, the throat frequently densely and finely papillate, the inside of the corolla sparsely hairy, sometimes

on the lobes or sometimes in the tube back of the filaments, or rarely the inside of the corolla glabrous; corolla-scales 1.5-2 mm. long, semi-ovate-lanceolate to linear-oblong and truncate above, or sometimes narrowed to a mere line, attached to corolla along one edge and to the base of the filament, the free margin glabrous or more or less ciliate and glandular; stamens 3-6 mm. long, generally a little unequal, the filaments sparsely long-hairy below the middle or glabrous, anthers 0.4-0.75 mm. long; style including branches 2-6 mm. long, the branches 1-3 mm. long, style and sometimes the base of the branches hirsutulous; ovary about 1 mm. long, very long-hairy, ovules 20-60; capsules 5-8 mm. long, ovate to elliptic-ovate, hirsute and sometimes sparsely glandular, beak generally prominent, the back of the valves not sulcate; seeds plump and subrotund, obtuse at ends, 0.5-1 mm. long, finely to coarsely pitted, sometimes tending to be transversely rugulose.

In California from sea level to 5000 ft., from dunes and sandy flats along the coast to clay slopes and rocky outcrops of arid interior hills and mountains, San Francisco and Contra Costa counties south to Los Angeles and San Bernardino counties and east to the southern Sierra Nevada foothills and western Mohave Desert.

The *P. Douglasii-stellaris* complex is closely related to the *P. curvipes-Davidsonii* complex, and although it is not quite so widespread, it is even more variable. Just as in the latter group where it seemed the better taxonomic procedure to recognize the smaller-flowered less variable component as a distinct species, so also in treating the *P. Douglasii* group it has seemed proper to recognize as a species the small-flowered Lower Californian variant. In distinguishing *P. stellaris*, we lack the more abundant material available when the study of *P. curvipes* was made, but from the relatively fewer collections available it would appear that *P. stellaris* is quite stable genetically, and in this regard it bears to the highly variable *P. Douglasii* much the same relation *P. curvipes* bears to *P. Davidsonii*. Besides the smaller flower, *P. stellaris* may be separated by the essentially different type of corolla-scales. In *P. Douglasii* these are always elongate and are attached throughout by one edge to the corolla-tube. In *P. stellaris*, the scales are tiny but they are either short and broad and attached along one edge or they are narrowly triangular and entirely free except at base. This free-tipped, linear-deltoid type of scale is found uniformly in *P. insularis* and I have regarded it as one of the remarkable features of that species. The fact that this type of scale should frequently occur in *P. stellaris* together with the scale of *P. Douglasii* in highly modified form seems especially significant and in my estimate of *P. stellaris* adds weight to its probable specificity.

In *P. Douglasii*, as thus restricted, there are several variants which stand out as perhaps deserving taxonomic recognition; but generally they have no geographic orientation and morphologically they merge so completely with the general complex that their separation has not been regarded as serving a useful purpose. One of the outstanding variants is that form with the leaf-segments again lobed or divided so that the leaf is at times bipinnatifid-dissected. Distinctive as extreme examples of this form are, no other character can be correlated with the variation and the occurrence of it from seaside dunes to near-

desert mountains adds neither ecologic nor distributional support. In many of the larger and more variable annual species of *Phacelia* marked variations in foliage occur, but I have regarded it as systematically undesirable and unsound to append to each of them nominal recognition of a variable that seems inherent in so many species.

Hence, when I recognize *P. Douglasii* var. *petrophila*, it is not restricted to small plants with entire or subentire leaves as it was originally described, but is enlarged to include an important and geographically distinct short-styled variant that is found on the west side of the San Joaquin Valley and bounding foothills. The rather rare plant which typified var. *petrophila* is probably itself a genetic entity, but when studied in connection with a considerable series of specimens, all are seen to be intimately related. The possible treatment of this inclusive entity as a species was considered but neither the morphologic variation nor the geographic break between it and typical *P. Douglasii* was regarded as sufficiently decisive.

KEY TO THE VARIETIES OF *P. DOUGLASII*

- A. Inflorescence finely to heavily glandular; filaments more or less hairy below the middle; style 4-6 mm. longvar. *eu-Douglasii*
 A. Inflorescence scarcely if at all glandular; filaments glabrous; style 2-3.5 mm. longvar. *petrophila*

3a. *P. DOUGLASII* (Benth.) Torr. var. *EU-DOUGLASII* Brand,

Pflanzenr. IV. 251: 114 (1913)

Eutoca Douglasii Benth., Trans. Linn. Soc. 17:276 (1835).*P. Douglasii* (Benth.) Torr., loc. cit.*P. Douglasii* (Benth.) Torr. var. *eu-Douglasii* Brand fma. *genuina* Brand, loc. cit.*P. Douglasii* (Benth.) Torr. var. *eu-Douglasii* Brand fma. *modesta* Brand, loc. cit., in part.

Plants generally green, more or less glandular especially in the inflorescence; leaves pinnately or bipinnately divided, generally with smaller divisions between the larger ones; corolla 7-13 mm. long, campanulate to rotate-campanulate; corolla-scales 1.5-2 mm. long, semi-ovate-lanceolate to narrowly oblong, truncate above, frequently ciliate with glandular or non-glandular hairs; stamens 3.5-6 mm. long, filaments more or less hairy below the middle; style generally 4-6 mm. long, the branches 1.5-3 mm. long.

The typical variety of *P. Douglasii* is found from seaside dunes to desert borders and in many small characters it is extremely variable. In the Gray Herbarium there are three plants labelled by Gray, "California Douglas," and although there is doubt about the origin of one of the plants, the other two were certainly collected by Douglas. Since they agree well with the original description, they are probably part of the type collection. These two plants correspond exactly to more recent collections of *P. Douglasii* made along the shores of Monterey Bay (cf. Elmer's at Bardin and Heller's at Seaside), and considering that Monterey was Douglas' headquarters during his California sojourn, it seems entirely likely that his plants came from the Monterey dunes. Other forms of *P. Douglasii* occur near Monterey (cf. *Abrams* No. 5206)

and throughout the South Coast Ranges where Douglas traveled, so the third plant in the Gray Herbarium reputedly Douglas' may easily have been collected by him.

Collections, all from California: Douglas (probably part of the type, G); near Antioch, Contra Costa Co., *H. L. Mason No. 5161* (CAS); Lake Merced, San Francisco Co., *Ewan 8703* (CAS), Cannon in 1892 (CAS); San Bruno Hills, San Mateo Co., *Eastwood 3750* (CAS); Ben Lomond sand hills, Santa Cruz Co., *L. S. Rose No. 33242* (CAS); near Boulder Creek, Santa Cruz Co., *L. S. Rose No. 39108* (CAS, G, NY, RSA); Bardin, Monterey Co., *Elmer No. 4573* (CAS, DS, F, M, P, UC, US, WS); near Seaside, Monterey Co., *Heller No. 6566* (CAS, DS, F, M, P); between Carmel and Pebble Beach, Monterey Co., *Abrams No. 5206* (CAS, DS, F, M, P, RSA, UC, US); San Antonio Mission, Santa Lucia Mts., Monterey Co., *Eastwood No. 4112* (CAS, US); Stone Canyon, 8 miles east of Salinas Valley, Monterey Co., *J. T. Howell No. 5952* (CAS, F); 8 miles from Coalinga on road to Priest Valley, Fresno Co., *H. L. Mason in 1930* (CAS, F, P); Cholame, San Luis Obispo Co., *Eastwood & Howell No. 2022* (CAS, F); Carrizo Plain near Painted Rock, San Luis Obispo Co., *Eastwood & Howell No. 4134* (CAS); Morro Bay, San Luis Obispo Co., *Giles in 1929* (CAS); Nipomo Mesa, San Luis Obispo Co., *Eastwood No. 14344* (CAS), *Eastwood & Howell No. 3880* (CAS, M, WS); 5.5 miles south of Oceano, San Luis Obispo Co., *Keck No. 2219* (CAS, DS); 5 miles south of Santa Maria, Santa Barbara Co., *L. S. Rose No. 37195* (CAS, M, NY, RSA); upper Sespe Creek, Ventura Co., *Munz No. 13150* (DS, F, P, UC); between Cuddy Ranch and Lockwood Valley, Ventura Co., *J. T. Howell No. 3858* (CAS, F, ND, NY, RSA, US, WS); Frazier Mt. Park Kern Co., *Winblad in 1941* (CAS); Three Rivers, Tulare Co., *L. S. Rose No. 40197* (CAS, RSA); near Palmdale, Los Angeles Co., *Eastwood & Howell No. 3964* (CAS, NY); near Elizabeth Lake, Los Angeles Co., *H. M. Hall No. 3063* (DS, F, M, P, UC); Wineville, Los Angeles Co., *Munz & Harwood No. 3834* (CAS, DS, P, UC, US); corollas small, perhaps varying toward *P. stellaris*).

A form from near San Lucas, Monterey Co., has the habit and aspect of var. *eu-Douglasii* but the small corolla and short style of var. *petrophila* (*Eastwood & Howell No. 2442*, CAS, P, UC). This may correspond to *Jepson No. 2677* which I have not seen but which is the collection first cited by Brand under his new form, fma. *modesta*.

Along the coast of Los Angeles County occurs a series of forms varying from *P. Douglasii* to *P. stellaris*, and it seems probable that the series has originated through hybridization since it is in this area that the ranges of the two species meet. Two collections have been seen which are typical *P. stellaris*, one from Redondo (*McClatchie No. 1347*, DS) and one from Playa del Rey (*Davidson No. 2333* in part, US), but other plants from both places are definitely intermediate (cf., Redondo, *Geis in 1909*, CAS, DS; Playa del Rey, *Davidson No. 2333* in part, US). Other collections from this same district that are more like *P. Douglasii* but that vary toward *P. stellaris* in some character or other are: Playa del Rey, *Braunton No. 831* (CAS, DS, US); *McClintock in 1938* (CAS); El Segundo, *MacFadden in 1935* (CAS), *Fosberg No. 8064* (CAS).

3b. *P. DOUGLASII* var. *PETROPHILA* Jepson Man. Fl. Pl. Calif. 826 (1925)

P. Douglasii (Benth.) Torr. var. *eu-Douglasii* Brand fma. *modesta* Brand, loc. cit. in part.

Plants generally somewhat canescent, scarcely if at all glandular, the hairs of the inflorescence and pedicels more or less spreading; leaves usually coarsely pinnately divided without smaller intermediate divisions or lobes, or leaves sometimes entire or with 1 or few salient teeth; corolla generally 6-9 mm. long, campanulate, the limb spreading only a little; corolla-scales narrowly linear, about 1.5 mm. long, sometimes reduced to a line or obsolescent; stamens 3-4 mm. long, filaments glabrous; style 2-3.5 mm. long, the branches 1-2 mm. long.

West side of the San Joaquin Valley and low bordering hills, San Joaquin County south to Fresno County in typical form; common in the upper San Joaquin Valley in Kern County but scarcely typical.

Collections, all from California: Corral Hollow at Castle Rock, San Joaquin Co., Hoover No. 2800 (UC); Los Bancos, Merced Co., Eastwood No. 14112 (CAS); Little Panoche, Fresno Co., Windblad in 1937 (CAS,UC); Mercy Hot Springs, Fresno Co., Eastwood & Howell No. 5116 (CAS,G,P,US); plains near Coalinga, Fresno Co., J. T. Howell No. 5863 (CAS,DS,NY,RSA); Oil Canyon, Fresno Co., J. T. Howell No. 5858 (CAS,F,G,P,US), Eastwood & Howell No. 2063 (CAS).

Jepson's original collection, which has not been examined, was made on the "surface of rock masses, Corral Hollow, Mt. Hamilton Range, 600 ft. (Jepson 9583, type)" (op. cit., p. 827).

A number of collections have been seen from the San Joaquin Valley which differ from var. *petrophila* in one character or another but yet are closely related to it. In general the plants are more or less glandular and occasionally the styles are longer. The following are representative of these variants: 8 miles west of Chowchilla, Madera Co., Hoover No. 526 (CAS,DS); open plains near Grapevine Grade, Kern Co., Peirson No. 11403 (CAS,FP,P); north slope of Tehachapi Pass, Kern Co., Peirson No. 5504 (CAS,FP), Munz No. 8955 (P); Oildale, Kern Co., Hoover No. 745 (CAS); Caliente Creek, Kern Co., Esau in 1935 (CAS); near Woody, Kern Co., Rowntree in 1938 (CAS); oilfields opposite Bakersfield, Kern Co., Heller No. 7585 (CAS,DS,F,M,P,UC,US).

A noteworthy variation in the seeds in the variety is the tendency for them to be more or less corrugated transversely. The effect is produced by a circular alignment of the pits, the lateral walls of which are lowered or are obsolescent.

4. PHACELIA STELLARIS Brand, Pflanzenr. IV. 251: 123 (1913)

P. Palmeri Vasey & Rose, Proc. U. S. Nat. Mus. 11:532 (1888), not *P. Palmeri* Torr. in Wats. Bot. U. S. Geol. Explor. 40th Par. (King's Exped.) 251 (1871).
P. Douglasii (Benth.) Torr. var. *cryptantha* Brand, *ibid.*, p. 114.

Root annual; stem branching widely at or near the base, hirsutulous with longer and shorter non-glandular hairs and rarely with a few capitate glands, especially in the inflorescence; leaves chiefly basal, pinnately divided, the divisions deltoid or oblongish, decurrent along the rachis and more or less confluent or the divisions more discrete and leaflet-like, obtuse, entire, or dentate-lobed, the blade oblong to oblanceolate, 1-8 cm. long, 0.5-2.5 cm. wide, pubescent with subappressed non-glandular hairs, petiole to 3 cm. long; racemes to 2 dm. long, laxly flowered, the flowers very distant below, more crowded above, pedicels elongate below, as much as 1.5 cm. long, the uppermost much shorter and only 2 or 3 mm. long; calyx in flower 3-4 mm. long, 1-2 mm. wide, oblanceolate-spatulate, obtuse, in fruit 5-8 mm. long, 1.3-2.5 mm. wide, oblong-oblanceolate, somewhat spatulate, obtuse or subacute, finely hirsute and hirsutulous, not glandular; corolla broadly campanulate, bowl-shaped, 3-5 mm. long, about 4.5 mm. across, tube 2 mm. long, conspicuously but finely hirsutulous-pilose outside on the lobes but apparently glabrous inside; corolla-scales small and variable, 0.3-0.5 mm. long, usually represented by free deltoid processes attached to the corolla only at the base or sometimes the scales broadly quadrate and attached to corolla-tube along one edge, usually glabrous, sometimes tipped by a long hair; stamens 2 mm. long, filaments glabrous, anthers 0.3-0.5 mm. long; style and branches 1-2 mm. long, the branches 0.5, the base

of the style and top of the ovary long-pilose, the hairs frequently as long as the style-branches; ovary nearly 1 mm. long, ovules 30-34; capsule ovate, 4.5-6 mm. long, 3 mm. wide, narrowed upward from broad base to prominent beak, a little compressed, long-hairy above, not nerved or sulcate on back of valves; seeds turgidly oval, 0.66 mm. long, nearly 0.5 mm. wide, ends rounded, coarsely pitted, the ridges between the pits joining in muriculate points.

Coastal dunes and sandy washes from Los Angeles Co., California, to San Quintin, Lower California.

Phacelia stellaris is distinctly a part of the *P. Douglasii* group and its close relationship to that species has already been discussed. The variations in the corolla-scales seem to indicate for *P. stellaris* a position intermediate between *P. Douglasii* and *P. insularis*, a remarkable species belonging to this same group.

Along the coast of Los Angeles County where the ranges of *P. stellaris* and *P. Douglasii* meet there are intermediates that are probably of hybrid origin. These have been discussed under *P. Douglasii* var. *eu-Douglasii*.

Representative collections. California: Playa del Rey, Los Angeles Co., Davidson No. 2333 in part (US); Downey cemetery, Los Angeles Co., Moskedahl in 1923 (P); Fairmont Park, Riverside Co., Wilder No. 873 (UC); San Diego, San Diego Co., M. E. Jones No. 3085 (first-cited collection of *P. Douglasii* var. *cryptantha*; CAS,DS,M,P,UC). Lower California: Tia Juana, Orcutt in 1882 (UC); Santa Maria Plains, 23.5 miles south of Hamilton Ranch, Wiggins No. 4323 (DS); 5 miles north of San Quintin, Epling & Robinson in 1935 (CAS,DS); San Quintin, Palmer No. 660 (type collection of *P. Palmeri* Vasey & Rose; CAS,ND,UC,US).

5. PHACELIA INSULARIS Munz, Bull. S. Calif. Acad. Sci. 31:113 (1932)

Root annual; stems simple below and few-branched or few- to several-branched from basal rosette of leaves, sometimes erect, frequently spreading and ascending, generally 1-3 dm. long with longer and shorter non-glandular hairs and sometimes minutely glandular-viscidulous above; leaves variable, entire to pinnately toothed or divided, the divisions oblong or rounded, obtuse, the larger divisions alternating with smaller lobes and more or less confluent with them, the blade lanceolate or oblong to ovate and elliptical, 1-7.5 cm. long, 0.5-3 cm. wide, hirsutulous with subappressed hairs, petioles to 6 cm. below, the uppermost leaves subsessile; racemes very laxly flowered, the lowest pedicels markedly elongate and 0.8-4.5 cm. long, recurved and spreading, the uppermost pedicels much shorter and about 3 mm. long; sepals in flower 4-5.5 mm. long, 1-2 mm. wide, in fruit strongly accrescent and subequal to markedly unequal, 8-16 mm. long, 1.5-9 mm. wide, oblanceolate to obovate-spatulate, chartaceous or coriaceous, more or less foliaceous, conspicuously veined, subacute, hirsutulous and sometimes a little viscidulous; corolla 6-11 mm. long, campanulate to rotate-campanulate, pubescent outside, minutely hairy inside, limb violet, tube whitish; corolla-scales deltoid to semi-ovate, attached to corolla at or near their base, 0.7-1.5 mm. long; stamens 3.5-5.5 mm. long, filaments glandular-puberulent except near the top, sometimes with a few long hairs near the middle, anthers 0.66 mm. long; style and branches 3-5.5 mm. long, the branches 1.3-2.5 mm. long, the style and sometimes the bases of

the branches hairy or glandular-hairy; ovary long-hairy, 1.3 mm. long, ovules 18-25; capsule strongly compressed, obovate, obtuse, 6-8 mm. long, 4.4-5 mm. wide, shortly beaked, the back of the valves prominently nerved; seeds ovateish to turgidly elliptical, obtuse or acute, 1-2 mm. long, rather finely pitted, brown.

Dunes of the California coast in Mendocino and Marin counties and on San Miguel and Santa Rosa islands off Santa Barbara County.

That so critical and distinctive a plant as *P. insularis* was not described until 1932 is quite as remarkable as the characters by which it is recognized. Even if it were strictly insular, we would expect that the early collectors on the islands would have found it; but, growing as it does in such localities as the Mendocino coast and Point Reyes which have been favorite fields for botanical collectors since the time of Bigelow and of Bolander, we wonder how it was overlooked, especially since it occurs abundantly at its mainland stations. One might almost imagine it a new creation if it were not that its distribution coincides with the occurrence of relict groves of closed-cone pines and that its characters indicate a primitive form.

Phacelia insularis is most nearly related to *P. Douglasii* and *P. stellaris* and I believe it is pointedly significant that the limits of distribution of the three species along the coast is exactly that of the Bishop Pine, *Pinus muricata*, except that the pine extends a little farther north to Humboldt County, California, and south to Cedros Island, Lower California; and of the three phacelias, *P. Douglasii* is the only one that extends any distance to the interior. On the coastal plains of Mendocino County, *P. insularis* is directly associated with the Bishop Pine, while in Marin County both the pine and phacelia grow on Point Reyes Peninsula. Although the pine is not known from San Miguel Island, both the pine and phacelia occur on adjacent Santa Rosa Island (cf. Howell, 1941, p. 6). Along the mainland coast of California, the distribution of *P. insularis* and *P. Douglasii* is exactly paralleled by the *Chorizanthe pungens* group, *C. Howellii* Goodman being an associate of the *P. insularis* at Fort Bragg; and yet another noteworthy species group whose distribution extends but little beyond that of the phacelias consists of the maritime wall-flowers of California. At first sight, it may be thought that the specific epithet *insularis* is rendered inappropriate by the present range extension to the mainland coast; but, when we consider the highly insular character of the distribution of the pine and associated plants from both a phytogeographic and also a paleobotanic point of view, the specific name *insularis* is seen to be peculiarly fitting.

While *P. insularis* seems to be most closely related to *P. Douglasii*, it is almost equally close to *P. divaricata*, and it might be interpreted as the modern representative of that ancient plant from which *P. Douglasii* and *P. divaricata* were derived. Certainly in foliage, inflorescence, and flower, *P. insularis* is like *P. Douglasii*, and the peculiar free corolla-scales of *P. insularis*, that are unlike any found in *P. Douglasii*, are frequently present in much-reduced form in *P. stellaris* which is itself so closely related to *P. Douglasii*. In characters of the fruit, however, *P. insularis* exhibits a definite relation to *P. divaricata*: the capsules in both are strongly flattened rather than turgid, and elliptical or obovate rather than ovate; and in both, the capsule-valves are conspicuously venulous-

nerved. While all discussions of phylogeny must be highly problematical, such a combination of characters as is exhibited by *R. insularis* is bound to excite the imagination of the student, who, groping amid the bewildering array of west American phacelias, seeks clues to possible relationship and descent on which to base a natural classification.

As might be expected, there are noteworthy differences in character between the plants of the island and mainland stations. In the north the plants are usually larger, although robust plants on San Miguel Island (cf. *Hoffmann in 1932*) are exceeded only by the most vigorous plants from Mendocino County. The size of the seeds increases gradually from south to north: on Santa Rosa Island the seeds are 1 to 1.3 mm. long; on San Miguel Island, 1.3 mm. long; at Point Reyes, 1.3 to 1.5 mm. long; and on the Mendocino coast, 1.5 to 2 mm. long. In reverse, the length of style and branches gradually diminishes from south to north (from 5 or 5.5 mm. to 3 mm.). These differences, emphasized by the significant geographic separation, are here interpreted as varietal.

KEY TO THE VARIETIES OF *P. INSULARIS*

- Corollas rotate-campanulate; seeds 1-1.3 mm. longvar. *typica*
Corollas open-campanulate; seeds 1.3-2 mm. longvar. *continentis*

5a. *Phacelia insularis* var. *typica* J. T. Howell, nom. nov.

P. insularis Munz, loc. cit.

P. curvipes Torr. var. *insularis* (Munz) Jepson Fl. Calif. 3: 269 (1943).

Plants usually erect, slender, and few-branched at or above the base; corolla 6-11 mm. long, rotate-campanulate; style and branches 5-5.5 mm. long, the branches 2-2.5 mm. long; seeds 1-1.3 mm. long, ovate to plumply elliptical, subobtusate or obtuse.

The following collections from the islands of San Miguel and Santa Rosa, California, have been examined: dunes on northeast part of Santa Rosa Island, *Munz No. 11756* (P, type: CAS frag.); Santa Rosa Island, *Moran No. 800* (CAS,DS); San Miguel Island, *Munz & Norris No. 11829* (P), *Hoffmann in 1930* (CAS), *Hoffmann in 1932* (P).

5b. *Phacelia insularis* var. *continentis* J. T. Howell, var. nov.

P. divaricata (Benth.) Gray var. *Wrangeliana* Jepson Fl. Calif. 3:270 (1943), as to plants, not *Eutoca Wrangeliana* F. & M.

Plantae saepe robustiores ramosae et decumbentes; corolla 5-8 mm. longa, late campanulata, haud rotata; stylo et ramis 3-4 mm. longis, ramis 1.5 mm. longis; seminibus 1.3-2 mm. longis, subovatis, acutis.

Type.—Herb. Calif. Acad. Sci. No. 298949, collected in loose sand of dunes on ocean bluffs, Fort Bragg, Mendocino Co., California, by J. T. Howell, No. 4226, May 25, 1929. Isotypes are in the following herbaria: DS, F, FP, G, M, ND, NY, P, RSA, UC, US, W, WS.

Other collections, all from California, that have been studied are: Point Reyes near the lighthouse, Marin Co., *J. T. Howell No. 4552* (CAS,F,NY,P,RSA,US,WS), *No. 4732* (CAS), *Ferris No. 8043* (DS,F,P,UC); Fort Bragg, Mendocino Co., *Seaholm in March, 1929* (CAS), *Seaholm in April, 1929* (CAS), *Heller No. 15324* (CAS,DS,M,P); Cleone, Mendocino Co., *Eastwood & Howell No. 2629* (CAS).

6. PHACELIA DIVARICATA (Benth.) Gray, Proc. Amer. Acad.
10:325 (1875)

Eutoca divaricata Benth., Trans. Linn. Soc. 17:278 (1835).

E. Wrangeliana Fisch. & Mey., Ind. Sem. Hort. Petrop. 2:37 (1836).

E. mexicana Hort. ex C. A. Mey. in Fisch. & Mey., ibid. p. 74, according to Ind. Kew. 1: 937.*

E. divaricata Benth. β. *Wrangeliana* (F. & M.) A. DC. in DC. Prodr. 9: 293 (1845).

P. divaricata (Benth.) Gray var. *Wrangeliana* (F. & M.) Jepson Fl. Calif. 3: 270 (1943), as to name, not as to plants.

Root annual; stem erect and simple or few-branched above, or more commonly widely branched and spreading from the base, 0.5-3.5 dm. long, puberulent and sparsely hirsute, rarely glandular; leaves mostly elliptic or narrowly ovate 1-5.5 cm. long, 0.5-3.5 cm. wide, hirsutulous and subtriglose, the pubescence subappressed above and more spreading below, entire or rarely with 1-4 lobes or divisions more or less pinnately arranged, acute at apex, cuneate at base, petioles to 6 cm. long, very short or almost none in the uppermost bract-like leaves; racemes more or less pedunculate, to 1.5 dm. long, flowers usually approximate or the lowest sometimes widely spaced, pedicels 1-3 mm. long, the lowest rarely longer; calyx-divisions in flower 4-6 mm. long, 0.66-1.5 mm. wide, in fruit much-enlarged, chartaceous and venulose, about equal in length, 10-12 (or 14) mm. long, 2-4 mm. wide, narrowly elliptic and oblanceolate to narrowly obovate, hirsute-ciliate, the faces hirsutulous and puberulent, obtuse or subacute; corolla lavender to violet, rotate-campanulate, generally 10-12 mm. long, sometimes only 7.5 mm. long or as much as 16 mm. long, the tube short, the limb broadly spreading; corolla-scales 2.5-4 mm. long, semi-lanceolate to narrowly semi-ovate, one edge attached throughout to corolla, the other edge free except at base where it is adnate to the filament; stamens 6-9 (or 11) mm. long, somewhat unequal, the filaments with few scattered long hairs and numerous short glandular processes, or the long hairs sometimes lacking, anthers 0.5-0.75 mm. long; style and branches 6-10 mm. long, the branches 2-3 mm. long, style somewhat hairy even up to the middle of the branches; ovary 1-1.5 mm. long, long-hairy, ovules 10-20; capsules 6-8 mm. long, broadly elliptic-oblong to ovate, obtuse or acute below short apiculation, flattened along sutures, some-

* Concerning the date of publication of the horticultural name *P. mexicana*, Miss Ruth D. Sanderson, Librarian at the Gray Herbarium, has written to me as follows:

"Our 'Ind. Sem. Hort. Petropol.' II begins with page 26 and the last page, which is obviously the end of II, is 54, and *Eutoca mexicana* appears nowhere. In the case of the other parts, as in III, the first twenty-nine pages contain a numbered alphabetical list of plant names only and *Eutoca mexicana* may have occurred there. Pages 26-54 of II are all descriptions. Dr. Johnston saw the complete copy in Berlin and on page 196 of the Journal of the Arnold Arboretum, vol. 16 (1935), he says that the Fischer and Meyer St. Petersburg seed-list for 1835 'bears a censor's date, Dec. 25, 1835, the equivalent of Jan. 5, 1836, of our present calendar.'

"In the list for 1842 (IX) and with the censor's date '10 Februarii, 1843' I found *E. mexicana* mentioned on page 74...."

Perhaps the reference in Index Kewensis given above concerns this entry of the name *E. mexicana* in the ninth St. Petersburg seed list for which the correct page but wrong serial number is given.

times subcarinate along middle, hirsute and puberulent, the valves venulose-nerved, the prominent midvein more or less distinctly branched above; seeds 1.25 mm. long, ovatis, brown, coarsely pitted.

Sandy coastal flats to clay and gravelly slopes and ridges of the interior, Mendocino County south to San Benito and Monterey counties, sea level to 3500 ft.

In both Herb. Gray. and Herb. Calif. Acad. Sci. are Russian specimens which are undoubtedly parts of the original collection of *Eutoca Wrangeliana*. In the Gray Herbarium one of the specimens is labelled "California. Ross." on one of the characteristic "Herb. Acad. Petrop." labels, and the specimen is quite like *Howell No. 6421* collected near Bodega Bay where there was once a Russian settlement. In Herb. Prager. at the California Academy are two specimens: one ticketed in the hand of Meyer himself "Nov Californ"; the other of garden origin bearing the letters Hpe., probably cultivated in the botanical gardens at St. Petersburg. These and other specimens indicate that *Eutoca Wrangeliana* is that form of *P. divaricata* in which the leaves are few-lobed, a variant of insufficient import to name. In character of fruit, however, the form of *P. divaricata* from the Sonoma County coast is quite like *P. insularis* var. *continentis* which grows on the coast of Mendocino and Marin counties to the north and south. In this form the capsule tends to be flattened and is broadly elliptical, while the cord-like vein on the back of the valves is not so evident. In general, the capsule is ovatis and less compressed and the valves tend to be a little carinate along the prominent midrib.

Representative collections: 10 miles west of Ukiah, Mendocino Co., *Cantelow in 1937* (CAS); mouth of Salmon Creek, 2 miles north of Bodega Bay, Sonoma Co., *J. T. Howell No. 6421* (CAS); Skaggs Springs, Sonoma Co., *Edwards in 1877* (CAS); upper St. Helena Creek, Napa Co., *J. T. Howell No. 15457* (CAS); St. Helena Palisades, Napa Co., *Jussel in 1937* (CAS); Mt. Tamalpais, Marin Co., *Eastwood in C. F. Baker distribution No. 3238* (F.G.M.P.UC.US), *J. T. Howell No. 2376* (CAS); Tiburon, Marin Co., *Eastwood in 1894* (G), in 1930 (CAS); Mt. Diablo, Contra Costa Co., *Brewer No. 1057* (G.UC.US), *Eastwood No. 4517* (CAS.US); Berkeley Hills, Alameda Co., *Fair in 1929* (CAS); Cedar Mt., Alameda Co., *J. T. Howell No. 1844* (CAS); Crystal Springs Lake, San Mateo Co., *C. F. Baker No. 432* (CAS.DS.F.G.M.ND.P.UC.WS); Emerald Lake, San Mateo Co., *L. S. Rose No. 37231* (CAS); Los Gatos, Santa Clara Co., *Heller No. 8429* (DS.F.G.M.US); Arroyo Bayo, Mt. Hamilton Range, Santa Clara Co., *C. W. & H. K. Sharsmith No. 1704* (CAS.UC), *No. 1985* (CAS.UC); Garcia Canyon, Monterey Co., *McCord in 1905* (CAS); near Hernandez, San Benito Co., *J. T. Howell No. 11171* (CAS).

The type of *Eutoca divaricata* was a collection "from California" made by David Douglas.

A remark concerning the date of publication of Bentham's important paper on the *Hydrophyllaceae* in the Transactions of the Linnaean Society of London, 1-5.5 cm. long, 0.5-3.5 cm. wide, hirsutulous and substrigose, the pubes were originally described there, *Eutoca divaricata*, *E. Douglasii*, and *E. phacelioides*. Brand (1913) gives the date as 1834, while Jepson (1943) gives both 1835 and 1837. In a preliminary remark to the General Index to the Transactions . . . vols. I. to XXV., it is stated that volume 17 part 2 of the Transactions, which contains Bentham's paper, was published in 1835.

7. PHACELIA CONGDONII Greene, Pittonia 5:22 (1902)

P. humilis T. & G. var. *Congdonii* (Greene) Macbr., Contrib. Gray Herb., n. ser., 49:38 (1917).

Root annual; stems simple at base, erect and few-branched above, or stems several and branching widely from basal rosette of leaves, mostly 1-2.5 dm. long, sparsely hirsute and hirsutulous, not at all glandular; leaves more or less clustered at the base, alternate and sparse above, elliptic to ovate, 1-4.5 cm. long, 0.5-2.5 cm. wide, hirsutulous and strigose, entire, or rarely with 1 or 2 small divisions at top of petiole, acute at apex, broadly cuneate, lower petioles to 3.5 cm. long, upper very short; racemes becoming elongate and to 8 cm. long, the flowers distant below, approximate above, pedicels 1-2 mm. long; calyx-divisions in flower 4-6 mm. long, 0.5-1.3 mm. wide, linear to linear-oblong, in fruit 5-12 mm. long, 0.66-2.5 mm. wide, linear-oblong to oblanceolate, hirsute and puberulent, not glandular; corolla pale to deep violet, 7-9 mm. long, open-campanulate, tube 4-5.5 mm. long; corolla-scales 1-2.5 mm. long, semi-triangular or semi-ovate at base, linear-attenuate above, plane or somewhat folded, edges of adjacent pairs free, at base attached to filaments about 1 mm.; stamens 3-5 mm. long, filaments tuberculate or sometimes smooth, anthers 0.5 mm. long; style including branches 4-5 mm. long, the branches 1-2 mm. long, the style hairy up to the branches; ovary 1-1.25 mm. long, long-hirsute, ovules 9-12; capsule ovate, attenuate into a prominent beak, 5.5-7 mm. long, pilose-hirsute and puberulent, the back of the valves with a prominent cord-like midvein; seeds ovate-oblong, 1.5 mm. long, dark brown, coarsely pitted.

Sandy soil of wooded slopes in the higher Sierra Nevada foothills and Tehachapi Mts. from Mariposa County south to Kern County, California, 2000 to 5000 ft.

Phacelia Congdonii is one of the less common phacelias of the Sierra Nevada and probably because it has been rare in collections it has not been well understood. Although Greene in the original description relates the plant to *P. Davidsonii* and thus properly removes it from *P. humilis* where Congdon placed the original collection, Macbride failed to appreciate the distinctive characters of Greene's species and returned the plant to *P. humilis* in the unfortunate varietal combination given above. Brand (1913, p. 115) makes *P. Congdonii* a synonym of *P. curvipes* and from his disposition of a collection of *P. Congdonii*, Purpus No. 5698, we know that Greene's species would be a part of his *P. curvipes* var. *pratensis* (1912, p. 222).

A detailed study of *P. Congdonii* has shown, however, that it is not immediately related to the *curvipes-Davidsonii* group but that it is so closely related to *P. divaricata* (Benth.) Gray that it is separated from it only with difficulty. When compared to the Coast Range *P. divaricata*, the Sierran *P. Congdonii* is noted as differing chiefly in the smaller parts of the flowers, and thus, in a quantitative rather than qualitative way, the two entities may be separated just as *P. curvipes* has been separated from *P. Davidsonii*, and *P. stellaris* from *P. Douglasii*. And, just as distributional considerations offered additional data by which these last four entities have been recognized as species, so also, the distinct geographic separation of *P. Congdonii* and *P. divaricata* has been an

important consideration in accepting *P. Congdonii* as a distinct species.

Phacelia Congdonii is not uniform throughout its range. In the north in Mariposa and Fresno counties, the plants are more slender and paler and the capsule and fruiting calyx are somewhat smaller. In the Greenhorn Range and Tehachapi Mts. in Kern County the plants are larger and somewhat greener and in appearance more closely resemble *P. divaricata*. The differences, however, do not seem sufficient for taxonomic recognition.

Representative collections, all from California. Buckeye, Mariposa Co., Apr. 25, 1895, Congdon (ND, type; DS); Pea Ridge road, Mariposa Co., Congdon in 1901 (CAS), in 1903 (M,US); Mormon Bar, Mariposa Co., Congdon in 1897 (DS,G); Big Sandy Valley, base of Black Mt., Fresno Co., Hoover No. 3466 (CAS,US); 2 miles from Miramonte on road to General Grant Park, Fresno Co., Wolf No. 4728 (CAS,F,G,NY,RSA,US); near Milo, Tulare Co., Dudley in 1900 (DS); Lock Ranch, Tulare Co., Winblad in 1938 (CAS); Greenhorn Pass, Kern Co., Purpus No. 5547 (M,UC,US); west slope of Greenhorn Range above Glenville, Kern Co., J. T. Howell No. 5097 (CAS), No. 5101 (CAS); Ft. Tejon, Kern Co., Abrams No. 11683 (DS); Tejon Canyon, Kern Co., Wolf No. 6343 (CAS,DS,F,FP,G,M,ND, NY,P,RSA,UC,US,WS).

8. PHACELIA PHACELIOIDES (Benth.) Brand, Pflanzenr. IV.

251: 117 (1913).

Eutoca phacelioides Benth., Trans. Linn. Soc. 17: 279 (1835).

P. circinaliformis Gray, Proc. Amer. Acad. 10: 325 (1875).

Root annual; stem erect, branching at base or above, 0.5-2 dm. tall, sparsely hirsute and puberulent, the shorter hairs dense and a little glandular; leaves elliptic-oblong, 1.5-4.5 cm. long, 0.5-1.5 cm. wide, prominently 4-veined on each side of midrib, strigose, entire (or 1 leaf with a pair of leaflets!), acute, cuneate at base, petiole 0.5-4.5 cm. long; racemes peduncled or subsessile, 2-8 cm. long, flowers crowded, pedicels 2-3 mm. long; calyx-divisions in flower 5 mm. long, 1-1.5 mm. wide, hirsute and puberulent, in fruit 12 mm. long, 1.5-3 mm. wide, oblanceolate, acute; corolla whitish, tubular with an expanded limb, 7 mm. long, lobes 2 mm. long, rounded, denticulate; corolla-scales variable even in one flower, semiquadrate, truncate or drawn upward into a narrow fold, plane or folded, united to base of filament, denticulate; stamens 2-2.5 mm. long, unequal, filaments hairy, anthers t'nv, 0.25-0.33 mm. long; style and branches 2 mm. long, branches a little unequal, about 1 mm. long, style hirsutulous; ovary 1 mm. long, hirsute, ovules 8; capsule 4 mm. long, ovate, gradually narrowed upward from a rounded base, somewhat compressed, the valves with prominent elevated midrib from the base for $1/5 - 1/3$ length of capsule, the median line veinless and shallowly and narrowly sulcate above; seeds plumply oblong or elliptic, scarcely angled, 1.5 mm. long, coarsely pitted, brown.

Steep rocky slopes in the northern part of the South Coast Ranges in Contra Costa and Santa Clara counties, California, 2000 to 4000 ft.

Fruiting characters of *P. phacelioides* point to a direct relationship between this localized endemic and the more widespread and variable *P. divaricata*, the fruiting calyces of the two being quite alike and the venation of the somewhat compressed capsules of the two bearing marked resemblances as well as differ-

ences. In young plants, the foliage pubescence of the two is similar, so that they closely resemble each other in aspect and differ chiefly only in the very unlike corollas. Because of its definite genetic stability and its apparent dependence on a specialized montane habitat, *P. phacelioides* is now restricted to a few isolated areas where the species has been able to persist since the Pleistocene orogeny of the California Coast Range province. In contrast, *P. divaricata* is much more variable and adaptable, and, growing as it does from seaside dunes to rocky-ridges and clay valley flats of the inner Coast Ranges, it has become the successful modern representative of this relationship in the region.

It is of interest to speculate on where Douglas might have collected the type of this species, whether on Mt. Diablo or on Mt. Hamilton. No morphologic difference has been detected between the plants from the two mountains, so, although a part of Douglas' collection has been available for study from Herb. Gray, it has not contributed anything pertinent to this particular problem. From the little that we know concerning the movements of Douglas in California (cf. Harvey, 1942, p. 161), it is apparent that he might have more readily climbed Mt. Hamilton from Mission San Jose, but it seems much more likely that Mt. Diablo was the mountain actually visited. One plant collected by Douglas which, it would seem, could have come only from Mt. Diablo is *Calochortus pulchellus* (Benth.) Dougl. (cf. Howell, 1938, pp. 116, 117), and yet another Mt. Diablo endemic of which Douglas apparently collected only a single plant is *Streptanthus hispidus* Gray (cf. Jepson, 1936, p. 37). Since this latter plant is one of the species which is restricted to the steep rocky and gravelly slopes near the summit of the mountain, the precise habitat where *P. phacelioides* grows, it seems almost beyond reason to doubt that Mt. Diablo is the type locality.

Representative collections. California, Douglas (G, type collection); Mt. Diablo, Contra Costa Co., Hall & Essig No. 10135 (CAS,DS,F,G,M,P,UC,US), Eastwood No. 4520 (CAS,US); Mt. Hamilton, Santa Clara Co., Parry in 1876 (G), Eastwood & Howell No. 9685 (CAS); along road from Mt. Hamilton to Livermore, Santa Clara Co., Eastwood No. 12466 (CAS); Sweetwater Creek, Mt. Hamilton Range, Santa Clara Co., C. W. & H. K. Sharsmith No. 3080 (CAS,UC,WS).

9. PHACELIA LINEARIS (Pursh) Holz., Contrib. U. S. Nat. Herb. 3:242 (1895)

Hydrophyllum lineare Pursh Fl. Amer. Sept. 1: 134 (1814).

Eutoca Menziesii R. Br. in Richards. Bot. App. Franklin Journey 764, tab. 27 (1823).

E. multiflora Dougl. ex Lindl., Bot. Reg. tab. 1180 (1828).

E. congesta Dougl. ex Lehm. Pugill. 2: 18 (1830).

E. echioides Dougl. ex Benth., Trans. Linn. Soc. 17: 278 (1835), nomen.

E. glomerata Dougl. ex Benth., loc. cit., nomen.

E. Menziesii α. *multiflora* (Dougl.) A. DC. in DC. Prodr. 9: 294 (1845).

E. Menziesii β. *congesta* (Dougl.) A. DC., loc. cit.

E. heterophylla Torr. in Stansbury, Explor. Utah 393 (1853).

P. Menziesii (R. Br.) Torr. ex Wats. Bot. U. S. Geol. Explor. 40th Paral. (King's Exped.) 252 (1871).

Plant an annual or winter annual; stem erect, branching at or above the base, the branches varying from substrictly erect to almost horizontally divaricate, 1.4 dm. tall, hirsutulous to hirsute, the hairs subappressed and ascending or the shorter ones softer and puberulent above, not glandular, frequently

cinereous; leaves rosulate at base or entirely scattered, the first two above the cotyledons opposite, the rest alternate, entire and linear to narrowly oblong or oblanceolate, or prominently and deeply parted with 1-4 narrow divaricate lobes, mostly 1-6 (or 8) cm. long, the blade or lobes to 1 cm. wide, hirsutulous to scabrous, the margins more or less revolute, the midvein impressed above and raised below, subobtuse to acute, narrowed at base into a narrowly to broadly bordered petiole or the leaves sessile; racemes thyrsoid-clustered at the top of the plant or the branches more open and corymbosely paniculate, the racemes becoming elongate and up to 1 dm. long, flowers rather crowded, the pedicels usually strongly ascending, 1-2 mm. long; calyx-divisions in flower 4-5 mm. long, 0.3-0.75 mm. wide, linear, in fruit 6-10 mm. long, 0.5-1 mm. wide, linear to linear-oblanceolate, hirsute and puberulent, not glandular; corolla lavender or pale violet, sometimes white, 6-7 mm. long, open-campanulate, throat 4 mm. long, minutely papillate; corolla-scales 2 mm. long, oblong-linear to semi-oblanceolate, one edge attached to corolla except at lobate or attenuate tip, the free edges connivent; stamens included or a little exserted, 5-6 mm. long, the filaments long-hairy near the top and minutely glandular-puberulent at base, anthers about 1 mm. long; style and branches 4.5-8 mm. long, the branches 1.5-3 mm. long, style and base of branches sparsely hirsutulous; ovary about 1 mm. long, ovules 11-14 (-22); capsules 6-7 mm. long, 3 mm. wide, ovate-triangular, gradually narrowed into a prominent slender beak, sparsely hirsutulous with a few scattered hirsute hairs, chartaceous and brittle, a little venulose, the back of the valves very shallowly sulcate; seed dark brown, 1.5-1.75 mm. long, ovate, acute, coarsely pitted.

Sandy or gravelly slopes and flats of western mountains and valleys from southern British Columbia and Alberta in Canada southward in the United States to California, Nevada, and Utah, 1000 to 6000 ft.

As has been indicated by Brand in his alignment of species in the subgenus *Eutoca*, *P. linearis* and *P. Franklinii* seem more closely related to certain perennial species than to any species treated in the present paper. In the review of the critical characters of *P. linearis*, however, it seems also to be related definitely to *P. divaricata*, and in the character of the capsule it is rather like *P. curvipes*. Since there is no definite character by which *P. linearis* can be excluded from this paper I have not only included it but also its near relative, *P. Franklinii*.

Although the technical characters of *P. linearis* indicate only a single entity, the plants are rather variable in habit, at times being quite strict with the flowers congested and again openly and paniculately branched. It was this diversity in habit which probably caused Douglas to name four kinds in his notes. Two were actually described while the other two were published as names by Bentham (l. c.) who gives all as synonyms of *Eutoca Menziesii* except the one published by Lehmann. In the Dudley Herbarium there is a photograph of the type of *Eutoca multiflora* Dougl. which is in the Lindley Herbarium, Cambridge University. The only collection data on the sheet are: "Northwest America. Douglas." The type of *Hydrophyllum lineare* was collected on the Lewis and Clark Expedition by Capt. Meriwether Lewis "on the banks of the Missouri."

Representative collections. Trail, British Columbia, *Macoun No. 66623* (CAS,F,ND,P); Pincher Creek, Alberta, *Moss No. 743* (UC); Missoula, Missoula Co., Montana, C. L. *Hitchcock No. 2321* (CAS,P,RSA); Crescent Hill, Yellowstone National Park, Wyoming, *H. L. Mason No. 3458* (CAS); Meadow Creek above Selway Falls, Idaho Co., Idaho, *Constance & Rollins No. 1649* (CAS); Salmon, Lemhi Co., Idaho, *Payson & Payson No. 1765* (CAS); City Creek Canyon, Salt Lake Co., Utah, *M. E. Jones No. 1723* (CAS,DS,F,ND,P,UC); Granite Mt. Pass, 11.5 miles east of Milford, Beaver Co., Utah, *Maguire No. 20992* (CAS); Keller Ferry, Ferry Co., Washington, *H. T. Rogers No. 368* (CAS); Rock Lake, Whitman Co., Washington, *Sandberg & Leiberg No. 116* (CAS,F,UC); Natches River near Edgar Rock, Kittitas Co., Washington, *Eastwood & Howell No. 3055* (CAS); Columbia River, Klickitat Co., Washington, *Suksdorf in 1881* (CAS,F); Cache Creek Bar, Wallawa Co., Oregon, *Constance, Rollins & Dillon No. 1551* (CAS); near Burns, Harney Co., Oregon, *Henderson No. 8706* (CAS); Crawfordsville, Linn Co., Oregon, *Haskin in 1929* (UC); Fandango Pass, Warner Mts., Modoc Co., California, *J. T. Howell No. 12081* (CAS,UC); near Omira, Lassen Co., California, *J. T. Howell No. 11848* (CAS,DS,ND); Loyalton, Sierra Co., California, *Eastwood No. 7841* (CAS); north side of Mt. Shasta, Siskiyou Co., California, *Cooke No. 15029* (CAS,DS); Hay Fork Valley, Trinity Co., California, *Tracy No. 6473* (CAS,DS,UC); Kings Canyon, Ormsby Co., Nevada, *C. F. Baker No. 895* (CAS,ND,P,UC); West Humboldt Mts., Pershing Co., Nevada, *Greene in 1894* (ND).

10. *PHACELIA FRANKLINII* (R. Br.) Gray Man. Bot. N. U. S.,
ed. 2, 329 (1856)

Euloca Franklinii R. Br. in Richards. Bot. App. Franklin Journey 764, tab. 27 (1823).

Plants biennials or winter annuals; stems strictly erect and unbranched or branched from the base and above with the branches strongly ascending, 1-6 dm. tall, sparsely hirsute and hirsutulous with longer and shorter non-glandular hairs; leaves densely clustered in a basal rosette or the rosette nearly absent, 1-6 cm. long and 0.5-2 cm. wide, pinnately parted, the segments entire or more or less deeply lobed, oblongish or lanceolate-deltoid, obtuse or acute, strigose and scabrous above, sparsely hirsutulous and hirsute below, margins plane or revolute, petioles to 3 cm. long; racemes capitate-congested at the ends of stems and branches or more laxly corymbose-paniculate or thyrsoid, the racemes densely flowered, to 5 cm. long, pedicels 1-2 mm. long; calyx-divisions in flower 5 mm. long, 0.5-0.75 mm. wide, linear, acute, in fruit much-enlarged, 9-10 mm. long, about 1 mm. wide, about equal, linear, subacute, hirsute and hirsutulous, not glandular; corolla lavender to violet with white throat, open- or rotate-campanulate, 6-9 mm. long, tube 2-3.5 mm. long, lobes crenulate, limb and upper part of throat minutely papillate, the corolla bristly-hairy behind base of filaments; corolla-scales 2 mm. long, cuneate, the truncate top denticulate, a little hairy at base, adjacent scales not connate; stamens 8 mm. long, the filaments sparsely long-hairy above the middle and with a few bristle-like hairs at base or filaments glabrous, anthers nearly 1 mm. long; style and branches 6 mm. long, the branches 1.5-2 mm. long, style hairy and glandular-puberulent to the branches; ovary 1.5-2 mm. long, long-hairy from near the base, ovules 27-45 on very irregularly lobed placentae; capsule narrowly ovate, 7.5 mm. long, 3.5 mm. wide, gradually narrowed to subacute top below prominent beak, back of valves shallowly sulcate; seeds narrowly ovate or oblongish, about 1.5 mm. long, brown, finely and shallowly pitted.

Mountain slopes, meadows, burns, and clearings, usually in gravelly soil,

widespread and frequently common, from Yukon and Mackenzie, Canada, southward in the United States to northern Minnesota and Michigan and to the central Rocky Mts. in northern Wyoming.

Phacelia Franklinii is most closely related to *P. linearis*, and, together with *P. mollis* Macbride, seems to connect *P. linearis* with *P. sericea* (Grah.) Gray. The most critical difference between *P. Franklinii* and *P. linearis* is found in the seeds. In *P. linearis* they are coarsely pitted and there is no suggestion of a lineal arrangement of the pits, while in *P. Franklinii* the pits are much smaller and are in rather definite lines. This same sort of arrangement of the pits is also found in *P. mollis* and *P. sericea*, but in those species the lines are emphasized by the thickened lateral walls of the pits which frequently form longitudinal ridges.

For a time it was believed that *P. mollis* Macbride (1917, p. 39) should be included in this present study since it shows so definite a relationship to *P. Franklinii* and is markedly different from *P. sericea* in its promptly deciduous corollas. In several critical characters, however, *P. mollis* is definitely allied to the *P. sericea* group, notably in the very long and strongly exerted stamens and styles and in the longitudinally striate seeds. Further information on the duration of the plant is needed: in the original description Macbride describes the plant as "biennis vel perennis," but there is nothing about the roots of two plants of the type collection (Coffee Creek, Yukon River, Yukon, *Eastwood No. 5512*) in Herb. Calif. Acad. Sci. to suggest more than biennial duration.

Together *P. Franklinii* and *P. linearis* extend southward from Arctic regions through the western part of North America to the central part of the Great Basin. In this vast subcontinental area, *P. linearis* is distributed over the southern and western part while *P. Franklinii* ranges far to the north, and, along the Canadian border, extends eastward to Lake Superior. These two species have the most extended distribution of any being treated in this paper and in the subgenus *Eutoca* the extent of their separate ranges is exceeded only by *P. sericea*.

Representative collections. Canada: between Whitehorse and Carcross, Yukon, *Eastwood No. 631a* (CAS); Great Bear Lake, Mackenzie, *Richardson* (cf. Raup, 1936, p. 291); Taltheilei Narrows, Great Slave Lake, Mackenzie, *Raup* (Raup, l.c.); Elbow River, Alberta, *Macoun No. 23775* (ND); Cornwall Bay, Lake Athabaska, Saskatchewan, *Raup* (Raup, l.c.); Prince Albert, Saskatchewan, *Macoun No. 12220* (F,P); Nipigon River, Ontario, *Macoun* (Macoun, 1884, p. 333); Bennett, British Columbia, *Cowles No. 991* (F).

United States: Vermilion Lake, Minnesota, *Sandberg* (Holzinger, 1896, p. 561); Isle Royale, Michigan, *T. C. Porter* in 1865 (F); Bonita, Montana, *Kirkwood No. 1255* (CAS,DS,F); 15 miles north of Butte, Montana, *J. T. Howell No. 7916* (CAS); Bonanza, Idaho, *Macbride & Payson No. 3467* (CAS,DS,P,UC); Birch Creek, Idaho, *R. J. Davis No. 1157* (CAS); Crescent Hill, Yellowstone National Park, Wyoming, *H. L. Mason No. 3450* (CAS); Big Horn Mts., Wyoming, *Rollins No. 486* (CAS).

Eutoca Franklinii was originally described as growing "abundantly amongst trees that have been destroyed by fire, on the banks of the river Mississippi." In Franklin's "Narrative of a Journey to the Shores of the Polar Sea," the name of this river is given as "the Missinnippi or Churchill River" (p. 180).

The Churchill River or Churchill Lake is the name now used for the elongate, lake-like body of water in northern Saskatchewan which lies to the east of Ile à la Crosse Lake. Franklin's expedition traveled along the Missinippi from June 17 to June 28, 1820.

11. PHACELIA VERNA Howell, Erythea 3:35 (1895)

P. Howellii Macbr., Contrib. Gray Herb. 49: 41 (1917).

A winter annual with the basal leaves rosulate or subrosulate; stem 5-15 cm. long, erect, branched from the base or simple below, branches one or several, rather strictly ascending, hirsutulous with longer coarser and shorter finer hairs and a few capitate glands; leaves ovate-lanceolate to ovate, 1-2 cm. long, 0.5-0.8 cm. wide, pubescence subappressed and scabridulous above, the veins impressed, the lower side more hirsutulous and glandular and the veins raised, entire or rarely with a small lobe or tooth, acute or subobtusate, the basal broadly cuneate or subtruncate at base, the upper narrowly cuneate, petioles bordered, short, to 8 mm. below, the leaves subsessile or sessile above; racemes 2-5 cm. long, flowers rather distant, appressed-ascending, pedicels 1-3 mm. long; calyx-divisions in flower unequal, about 3 mm. long, 0.5-1 mm. wide, in fruit very unequal, 5-7 mm. long, 0.6-1.6 mm. wide, linear to oblanceolate, somewhat strigose and hirsutulous and puberulent, capitate glands few; corolla white or lavender, 5-6 mm. long, open-campanulate, the tube inside bearing a few long hairs on the veins between scales; corolla-scales free, nearly 1 mm. long, semi-oblong to semi-ovate, plane or a little folded above, at base attached to filament, glabrous and entire or long-ciliate below and crenulate above; stamens exserted, 6.5 mm. long, the filaments smooth and glabrous, anthers 0.5-0.7 mm. long; style and branches 6 mm. long, the branches 5 mm. long, the style and base of branches hairy; ovary 1 mm. long, rather densely short-hirsutulous, ovules 6-11; capsule ovate, 5 mm. long, acute below the rather prominent beak, hirsutulous, not glandular, valves shallowly sulcate on back; seeds oblong to ovate, 1.25 mm. long, acute, brown, coarsely pitted.

Rocky ridges and wet cliffs in the Umpqua Valley, Douglas Co., Oregon.

After mistaking for *P. verna* the phacelia I have named *P. Peckii*, Macbride redescribed Howell's most excellent species as *P. Howellii*. The root of this mistake will probably be found in Brand's treatment where *P. verna* is referred to *P. Pringlei* as *forma placensis pluriovulatis* (1913, p. 117). Actually the relationship between *P. verna* and *P. Pringlei* is not very evident although I believe that a real connection is to be discerned in such characters as the unequal calyx-divisions, the open-campanulate corolla, and the shallowly sulcate valves of the capsules. The plant is markedly divergent, however, in such characters as its winter-annual habit and its conspicuously hairy corollatube. The habitat seems to be as highly specialized as the plant since it is locally confined to rocky ridges and wet cliffs of the Umpqua Valley.

Collections, all from Douglas Co., Oregon: near Roseburg, *Howell No. 1516* (type collection of *P. verna*, D.S.M.N.D.U.C.W.S.; these specimens were collected on two days, some on May 1, 1887, some on May 5); wet cliff 12 miles north of Roseburg, *Peck No. 14801* (W); moist crevices of basaltic rock near summit of Tyee Mt., 2500 ft., Umpqua Valley, *Cusick No. 4022* (W.S.); Oregon, *J. & T. J. Howell No. 369* (G, type of *P. Howellii*).

12. PHACELIA PECKII J. T. Howell, Leaf. West. Bot. 4: 25 (1944)

P. Pringlei of Oregon references, not Gray.

P. verna of Macbride, Contrib. Gray Herb., n. ser., 49: 40 (1917), not Howell.

Root annual; stems slender, erect, 5-15 cm. tall, often purplish-tinged, hirsutulous and capitate-glandular, the stem below the first pair of foliage leaves often elongate, the branches few, generally substrictly ascending; leaves rather few and scattered, narrowly oblong to lanceolate, 1-2.5 cm. long, 0.2-0.5 cm. wide, substrigillose above, glandular-hirsutulous below, subacute, at base attenuate into a narrowly bordered petiole, petiole mostly 0.5-1.5 cm. long; racemes substrict and scarcely flexuose, 2-4 cm. long, the flowers approximate, pedicels 1-3 (or 5) mm. long; calyx-segments in flowers 2 mm. long, 0.25-0.5 mm. wide, in fruit strongly unequal, 3-6 mm. long, 0.25-1 mm. wide, linear to oblanceolate, hirsutulous and glandular, the apex straight and plane; corolla violet, broadly rotate-campanulate, 5-6 mm. long, the tube about 2 mm. long, the lobes subentire; corolla-scales 1 mm. long, oblong, quadrate, the free edges of adjacent pairs connate; stamens 5 mm. long, the filaments bearing numerous elongate hair-like subretorse processes, the anthers 0.66 mm. long; style and branches 4-5 mm. long, the branches 3-4 mm. long, the style and base of the branches hairy; ovary 1 mm. long, ovules 8-11; capsule generally elliptic-ovate, 4 mm. long, subacute below the apiculation, sparsely hirsutulous and a little glandular, the hairs longer and shorter, the valves longitudinally sulcate on the back; seeds subovate, acutely angled, 1-1.5 mm. long, dark brown, finely and minutely reticulate-pitted.

Phacelia Peckii is not uncommon in the mountains of southern Oregon in Jackson and Josephine counties where it grows on moist slopes. Prof. Peck (1941, p. 592) also reports it (under the name *P. Pringlei*) from Klamath County, but no specimen has been examined from there.

Representative collections, all from southern Oregon. Moist ground near the top of Grizzly Peak, Jackson Co., *Peck No. 3291* (CAS, type: W); Dead Indian Creek, 5000 ft., Jackson Co., *Applegate No. 2426* (DS,US); Corral Creek Falls, Chinquapin Mt., Jackson Co., *Applegate No. 4340* (DS,W); moist soil, western Cascades, Jackson Co., *Cusick No. 2870* (CAS,DS,F,G,M,P,UC,US); moist ground, 17 miles east of Ashland, Jackson Co., *Peck No. 15006* (DS,W); Grizzly Range east of Medford, Jackson Co., *Leiberg No. 4157* (US); Waldo, Josephine Co., *Howell in 1884* (CAS, M,ND,US,WS); Illinois River, Josephine Co., *Rattan in 1879* (DS,G).

Although *P. Peckii* differs from *P. Pringlei* in small details in almost every structure regarded as critical in the study of *Phacelia*-species, Macbride is apparently the only botanist who has indicated even a few of the differences between the two (1917, p. 40). These differences were discussed under the name *P. verna*, for not only did Macbride mistake *P. Peckii* for Howell's species but he redescribed *P. verna* under the name *P. Howellii* (ibid., p. 41). Two of the most important differences, however, between *P. Pringlei* and its relative in southern Oregon were overlooked by Macbride, namely, the conspicuously barbate filaments and the smaller finely reticulate-pitted seeds. In habit, the two are quite unlike and usually a glance suffices to indicate the placement of a specimen.

13. PHACELIA PRINGLEI Gray, Proc. Amer. Acad. 17:223 (1882)

Slender erect annuals 0.5-1.5 dm. tall with the hypocotyle and first internode frequently elongate and sometimes exceeding in length the upper branched part of the plant, the branches tending to be subumbellately clustered above the first foliage leaves and more or less flexuously spreading, slender and wiry, the hypocotyle hirsutulous, the stem above the cotyledons finely hirsutulous and capitate-glandular; leaves linear to narrowly oblanceolate, 1-2.5 cm. long, 1-5 mm. wide, hirsutulous and sparsely glandular, entire or undulate, acute or subobtusate, attenuate at base into longer or shorter bordered petiole, petiole to 1 cm. long; racemes elongate slender and somewhat flexuous, to 8 cm. long, rather openly flowered, pedicels 1-2.5 mm. long; calyx-divisions in flower 1.5-2 mm. long, 0.2-0.3 mm. wide, in fruit more or less unequal, one usually much smaller than the others 3-5.5 mm. long, 0.25-0.66 mm. wide, linear to oblanceolate-spatulate, glandular and hirsutulous, outwardly curving at the top; corolla pale lavender, rotate-campanulate or saucer-shaped, 3-4 mm. long, the tube 1.5 mm. long; corolla-scales semi-ovate or quadrate, 0.5-0.66 mm. long, the free edges of adjacent scales between filaments connate; stamens 3-3.5 mm. long, filaments bearing flattened retrorse triangular processes, these sometimes attenuate at top, anthers about 0.3 mm. long; style and branches 3.5-4 mm. long, the branches 2.5-3 mm. long, the style and lower part of the branches hairy; ovary 0.66 mm. long, ovules 4-7; capsule 3 mm. long, generally subglobose and obtuse below the apiculation, sparsely long and short hairy and a little glandular, the back of the valves prominently longitudinally sulcate; seeds ovate or semi-ovoid, 1.5-1.66 mm. long, light brown, the pitting rather coarse.

High slopes of the Scott Mts. between Siskiyou and Trinity counties, 6000 to 7500 ft.

Apparently endemic to one of the higher ridges of the Klamath Area (cf. Jepson, 1925, pp. 10, 12), *P. Pringlei* was the first of a series of widely dispersed but closely related species to be described. Immediately related to *P. Pringlei* are *P. Peckii* and *P. Leonis*, the two species which occur in the same general area with *P. Pringlei* in northern California and southern Oregon. *Phacelia minutissima* Henderson has been found far to the north and east in three widely separated places in Nevada, Idaho, and northeastern Oregon; and locally isolated in the high southern Sierra Nevada in California is *P. orogenes* Brand. The rare endemic phacelia of the Umpqua Valley, Oregon, *P. verna* Howell, may be related to the *P. Pringlei* group, but the connection is not so evident; and the same holds for the rare and anomalous *P. Greenei* Howell which is intermediate between *P. Pringlei* and *P. humilis* and which has been found only in northern California (Howell, 1943, pp. 17, 18). Undoubtedly *P. racemosa* (Kell.) T. S. Brandg. of the northern and middle Sierra Nevada has also been derived directly from the *P. Pringlei* complex, although it is referred to the subgenus *Euphacelia* because of its biovulate plantaeae.

This disrupted distribution of related entities would seem to indicate that *P. Pringlei* and its immediate relatives are the modern representatives of an old complex that was widespread and perhaps more common through the central

Pacific area of North America preceding Pleistocene glaciation. Both the period of successive glaciations and the preceding period of profound orogenic activity in western America would adequately account for the present isolation of the species with their present-day distribution centering in the geologically significant Klamath Area.

Collections, all from California. Mountains about the headwaters of the Sacramento River, 7,500 ft., Aug. 20, 1881, *Pringle* (G, type; F), at 7,000 ft., Sept. 1, 1882, *Pringle* (CAS,F,M,ND,UC,US); Scott Mt., between Trinity and Siskiyou counties, *Engelmann* in 1880 (M), *J. T. Howell* No. 13612 (CAS,F,G,P,US,W); Mt. Eddy, Siskiyou Co., *Eastwood* No. 1993 (CAS), *Heller* No. 13571 (DS); "near Mt. Shasta," *Lemmon* in 1879 (CAS,F,ND,UC,US).

14. PHACELIA OROGENES Brand, Beilage, Jahresb. Kgl. Gymnas.

Sorau, 7 (1911)

P. Pringlei Gray var. *orogenes* (Brand) Jepson Man. Fl. Pl. Calif. 827-8 (1925).

Root annual; stem 2-10 cm. long, slender, few-branched near the base or simple below and few-branched above, hirsutulous and a little glandular, the glandular hairs more numerous in the inflorescence; leaves opposite below, alternate above, linear-lanceolate, entire, acute, gradually attenuate below into more or less bordered and indeterminate petiole, blade and petiole 1-3.5 cm. long, 1-4 mm. wide, hirsutulous and glandular; racemes laxly few-flowered, up to about 5-flowered and to about 4 cm. long, pedicels 2-8 mm. long; calyx-divisions in flower unequal, 2-3 mm. long in one flower, linear-oblancoate, acute, in fruit markedly unequal, the shortest 3.5-5 mm. long and linear, the longest 5-9 mm. long and linear-oblancoate, hirsutulous and glandular; corolla rotate-campanulate, 4-6 mm. long, 5-7 mm. across, limb violet, tube white; corolla-scales oblongish, 1 mm. long, attached at very base to filaments; stamens 3.5 mm. long, filaments glabrous, anthers nearly 0.5 mm. long; style and branches 3.5 mm. long, the branches nearly 3 mm. long, style hairy to the branches; ovules 6-8; capsule broadly oval or roundish, 3 mm. long and nearly 2.5 mm. wide, obtuse below apiculation, the back of the valves longitudinally sulcate; seeds broadly ovate, 1.75 mm. long, pitted, brownish.

Subalpine meadow borders and moist slopes of the Sierra Nevada in Tulare County, California, 8000 to 10,000 ft.

Phacelia orogenes is generally rather diffusely and characteristically branched and the stems and inflorescence are slender and flexuous; but occasionally the plants are more stiffly branched or strictly erect and then the plants closely resemble *P. minutissima* or *P. Peckii*. In very reduced individuals growing in unfavorable situations, the slender stems bear only a single flower.

From a phytogeographic point of view, *P. orogenes* is a most interesting species, isolated as it is in the higher part of the southern Sierra Nevada. Because it is so definitely related to *P. Pringlei* of the long-persistent Klamath highland of northwestern California, geologic considerations attendant on its origin and dispersal must be the same as pertain to other plants exhibiting a like distribution pattern. The most noteworthy of these is the Foxtail Pine, *Pinus Balfouriana*, and it is indubitably certain that the geographic and cli-

matic arrangements in geologic time that have effected the bifarious distribution of this remarkable pine have also been responsible for the isolated occurrence of *P. oregones* in an area so far removed from its nearest relatives. Together with a few other associated plants, the pine and phacelia undoubtedly weathered the successive advances of the ice during the late Pleistocene on the extensive unglaciated areas in the southern Sierra Nevada; and although the phacelia is now found only in canyons carved by the ice-streams, it is there today because it probably cannot endure the more rigorous climate of the elevated unglaciated uplands which are now mostly above 10,000 feet.

Collections, all from Tulare County, California: Eagle Lake Trail near Mineral King, the type locality, *J. T. Howell No. 17160* (CAS); Mineral King, *T. S. Brandegee in 1892* (UC), *J. T. Howell No. 17108* (CAS); between Pinto Lake and Black Rock Pass, *J. T. Howell No. 17346* (CAS), *Ferris & Lorraine No. 10923* (CAS,DS); between Big Arroyo and Chagoopa Plateau, *J. T. Howell No. 17435* (CAS); Lost Canyon, *J. T. Howell No. 17771* (CAS). Numerous duplicates of my collections have been distributed. The type, which has not been examined, was collected on a "moist hillside on Eagle Lake Trail (Hall u. Babcock n. 5354)," near Mineral King.

15. PHACELIA LEONIS J. T. Howell, Leaf. West. Bot. 3:206 (1943)

A small and frequently inconspicuous annual herb, 2-12 cm. tall; stem erect with the branches spreading a little, the stem often elongate below the first foliage leaves, the hypocotyle hirsutulous, the first internode and above hirsutulous and capitate-glandular; leaves few, linear to linear-oblong or linear-lanceolate, 0.5-3 cm. long, 1-4 mm. wide, hirsutulous and capitate-glandular, entire, acute, narrowly cuneate-attenuate at base into a narrowly margined petiole, petiole about 3 mm. long; racemes 1-9 cm. long, generally a little spreading but not flexuous, flowers rather close together or sometimes the lowest flowers more distant, pedicels 1-2 mm. long or shorter; calyx-divisions about 2 mm. long and 0.5-1 mm. wide in flower, accrescent and very unequal in fruit, 4-7 mm. long, 0.5-1.2 mm. wide, linear to oblanceolate, glandular-hirsutulous; corolla pale lavender, openly campanulate, 2-3 mm. long, tube 1 mm. long, lobes a little crenulate; corolla-scales small or sometimes obsolete, about 0.5 mm. long, the margins free or connate; stamens 1.75-2 mm. long, filaments glabrous or finely and sparsely hairy, anthers about 0.25 mm. long; style and branches 2 mm. long, the branches 1.3 mm. long or distinct nearly to the base, style glabrous; ovary sparsely long-pilose and glandular, 0.6 mm. long, ovules 6-8; capsule broadly elliptic, 3-3.5 mm. long, 2-2.5 mm. wide, obtuse, shortly apiculate, hirsutulous and sparsely capitate-glandular near the top, the back of the valves longitudinally sulcate; seeds subovate, 1.75 mm. long, rather coarsely pitted.

Moist slopes and sandy flats in the mountains of Trinity and Siskiyou counties in northwestern California, 5500 to 6500 ft.

This remarkable little phacelia is closely allied to *P. Pringlei* and in a more conservative view of that species it might be regarded as a variety. It differs, however, in characters other than the much smaller and differently shaped corolla, notably in the broader and more coriaceous fruiting calyx-segments, in the shorter stamens and style, and in the differently shaped capsule. Although

P. Leonis is to be directly related to *P. Pringlei* both morphologically and geographically, it bears a striking resemblance both in structure and in aspect to the rare *P. minutissima* Henderson of Idaho, Nevada, and northeastern Oregon; and, because of its intermediate character it connects the heretofore anomalous *P. minutissima* directly to the *P. Pringlei* complex.

Collections, all from California: Open hillside, summit of Siskiyou Mts. on Takilma-Happy Camp road, 5500 ft., Siskiyou Co., *Hitchcock & Martin No. 5217* (CAS, type; Herb. Univ. Wash.); sandy moist soil by stream in open situations, Mary Blaine Mt., 6400 ft., Siskiyou Co., *Tracy No. 14443* (CAS, UC); sandy soil, Union Lake, Salmon-Trinity Mts., Trinity Co., *H. M. Hall No. 8613* (UC).

16. *PHACELIA MINUTISSIMA* Henderson, Bull. Torr. Bot. Club
27:351 (1900)

P. foliosepala Nels. & Macbr., Bot. Gaz. 55: 377 (1913).

Root annual; stem erect, 3-10 cm. tall, hirsutulous and a little glandular, branched at or above the base, the branches more or less erect-ascending or substrictly erect; leaves opposite below, alternate above, linear-oblongate or oblanceolate, the largest about 1 cm. long, 2-3 mm. wide, the lower ones smaller and broader in proportion to length, hirsutulous and sparsely glandular, entire, acute, attenuate at base into a short more or less bordered petiole, petiole about 2 mm. long; racemes rather loosely few-flowered but the flowers substrict, pedicels 3-9 mm. long or sometimes shorter; calyx-divisions in flower 3 mm. long, linear-oblong, hirsutulous, in fruit much-enlarged, one frequently foliaceous and much longer than the others, in the same flower 6-12 mm. long and 0.5-2.5 mm. wide, glandular and hirsutulous; corolla lavender, tubular, 3-4 mm. long, the limb spreading a little; corolla-scales 0.5 mm. long, semi-linear-lanceolate; stamens about 1.5 mm. long, nearly equal, filaments glabrous, anthers 0.25 mm. long; style about 1 mm. long, the branches about 0.5-0.6 mm. long; ovary 1 mm. long, hirsutulous above, ovules 11 or 12; capsule 5 mm. long, ovate or elliptic, acute or subobtusely beaked, the back of the valves shallowly longitudinally sulcate; seeds nearly 1.5 mm. long, finely pitted.

Moist slopes and flats in mountains of the northern part of the Great Basin in Oregon, Idaho, and Nevada, 5500 to 8000 ft.

The relationship of *P. minutissima* has been variously interpreted, and, until it was definitely allied to the *P. Pringlei* group with the discovery and description of *P. Leonis*, I regarded it as anomalous since not even in its geographic distribution was there a clue to suggest remotely its affinity. Originally Henderson placed it "very near" *P. saxicola* Gray, and Brand (1913, p. 118) did little better when he placed it between *P. cephalotes* Gray and *P. demissa* Gray, while Nelson and Macbride (*op. cit.*, p. 378), in discussing their new species, *P. foliosepala*, expressed the opinion that in the section *Eutoca* "there seems to be no species nearer to it than *P. linearis* (Pursh) Holz." Through *P. Leonis*, however, *P. minutissima* is definitely related to the *P. Pringlei* group and the seeming incongruity of its distribution is quite in accord with the distribution of that group when it is considered from the viewpoint of geologic history. This I have discussed briefly under *P. Pringlei*.

Collections. Dry gravelly or rocky ground, Soldier Mt., 8,000 ft., Blaine Co., Idaho, *Henderson No. 3386* (type collection, G,NY,US); moist sunny flats, Gold Creek, 6,300 ft., Elko Co., Nevada, *Nelson & Macbride No. 2232* (type collection of *P. foliosepala*, G); Cattle Camp at head of Horse Creek, 5,400 ft., Wallowa Co., Oregon, *Sheldon No. 8360* (US,CAS frag.); moist flat near Buckhorn Spring, Wallowa Mts., Wallowa Co., Oregon, *Peck No. 18310* (W).

17. *PHACELIA VALLICOLA* Congdon ex Brand, Beilage, Jahresb. Kgl.

Gymnas. Sorau 7 (1911)

P. curvipes Torr. var. *yosemitana* Brand, Univ. Calif. Publ. Bot. 4:222 (1912).

Root annual; stems erect, 0.5-3 dm. tall, simple below with few ascending branches above, or few- to many-branched from the base, hirsutulous, hirsute, and glandular, the longer hairs and the capitate glands fewer; leaves opposite below and alternate above, somewhat clustered near the base, rather distant above, elliptic to ovate, 0.7-4 cm. long, 0.3-1.5 cm. wide, hirsutulous and glandular, the chief veins impressed above and raised below, acute, rounded to cuneate at base, petiole 0.5-2.5 cm. long, or in the uppermost reduced leaves very short; racemes solitary or paired at the end of branches, few-flowered and about 1 or 2 cm. long, or many-flowered and up to 7 cm. long, pedicels mostly 2.5 (or 10) mm. long, straight or somewhat curving; calyx-divisions in flower unequal, 3.5-5 mm. long, 0.3-1.3 mm. wide, in fruit strongly accrescent, very unequal, 6-9 (or 15) mm. long, 0.5-3 mm. wide, linear to oblanceolate-spatulate, glandular-hirsute; corolla violet, tubular-campanulate with limb somewhat spreading, 5-6 mm. long, the tube about 3 mm. long, the lobes crispy-undulate; corolla-scales 1 mm. long, quadrate, the free edges of adjacent pairs connate with the line of union extending upward as a marked apiculation, or the scales distinct and widened upward, at base attached to filaments; stamens included, nearly equal, about 2.5 mm. long, filaments roughened by retrorse processes, anthers nearly 0.5 mm. long; style and branches nearly 2.3 mm. long, style hairy up to branches, the branches 1.3 mm. long; ovary about 1 mm. long, densely hirsute with long hairs, ovules 18-25; capsule hirsute, broadly and turgidly ovate, 6 mm. long including the persistent beak-like base of style, beak 2 mm. long, the back of the valves with a median longitudinal impressed line; seeds mostly triangular-ovate, 1.5-2 mm. long, light brown, coarsely and shallowly pitted.

Sandy or gravelly soil of mountain slopes or flats, Tuolumne and Mariposa counties, California, 2000 to 5500 ft.

Although in the original description and later in his taxonomic treatments Brand related *P. vallicola* to *P. Purpusii*, the fact that he also described as a variety of *P. curvipes* specimens that are quite typical of *P. vallicola* indicates the rather anomalous position occupied by *P. vallicola*. After a detailed comparison of the species involved, it would appear that while *P. vallicola* is probably not directly related to *P. Purpusii*, it does bear a definite relation to the *P. Pringlei* group and that it must also be related to *P. curvipes* because of several important characters. Whereas *P. vallicola* lacks the peculiar corolla and the elongate stamens and styles that make so definite a group of *P. Purpusii*, *P. grisea*, and *P. mohavensis*, it is related to them and to the *P. Pringlei*

group in general because of the markedly unequal calyx-segments and the retrorsely roughened filaments. In the critical character of the capsule, however, *P. vallicola* bears a definite relation to *P. curvipes*, a relation that is borne out when one compares the habit and appearance of less robust entire-leaved individuals of the Sierran plant with normal specimens of the desert plant. In both, the capsule is turgidly ovate with a prominent flattened tapering beak and the valves in *P. vallicola* and generally in *P. curvipes* bear a median longitudinal impressed line. There is a tendency in *P. vallicola* for the pedicels of the lowest flowers to be a little longer and divaricately curving as is so characteristic in *P. curvipes*, but the pedicels are usually not so long or spreading as they are in *P. orogenes* which is definitely allied to the *P. Pringlei* group. It may be that *P. vallicola* originated from a fertile cross between members of the *P. Pringlei-curvipes* groups, but, if it did, it must have been very long ago since formidable geographic barriers now exist between probable parents and the progeny is itself a rare isolated plant. For matters of convenience as much as anything, *P. vallicola* is left among species of the *P. Pringlei* group in this treatment.

Representative collections, all from Mariposa County except the first. Strawberry Lake, Pine Crest, Tuolumne Co., *Quick No. 43-11* (CAS); D. B. Wiggins in 1934 (CAS,DS,G,ND,RSA); Hite's Cove, Congdon in 1892 (type collection; DS,G,UC); Hennessey's place, Merced River Canyon, J. B. Lumbert in 1894 (DS,G,UC); Yosemite Valley, Parry in 1881 (DS,US); Tenaya Trail, 5,300 ft., H. M. Hall No. 8951 (UC, type of *P. curvipes* var. *yosemitana*); Snow Creek Trail (i.e., "Tenaya Trail"), 5,500 ft., J. T. Howell No. 15563 (CAS); Indian Creek, Yosemite Valley, Osgood in 1930 (CAS). Specimens grown from seed collected at Strawberry Lake, Tuolumne County, by C. R. Quick in 1942, are in Herb. Calif. Acad. Sci.

18. PHACELIA PURPUSII T. S. Brandg., Bot. Gaz. 27:451 (1899)

P. humilis T. & G. var. *calycosa* Gray, Proc. Amer. Acad. 10: 318 (1875).

P. trichostemoides Greene ex Brand, Das Pflanzenr. IV. 251: 103 (1913), in synonymy.

Root annual; stems erect, simple at base and few-branched above or branching from the base, the branches ascending or widely spreading, 1-3.5 dm. tall, finely hirsutulous and glandular-villous, not at all hispid; leaves rather few, narrowly oblong to ovate, 1.5-6 cm. long, 0.4-3 cm. wide, glandular and hirsutulous, entire or with 1-3 salient teeth or short lobes or sometimes the blade irregularly pinnately divided, petioles 1.5-4 cm. long or the upper almost lacking; racemes substrictly ascending, to 1.5 dm. long, rather densely flowered, pedicels 1-2 mm. long; calyx-divisions very unequal, in flower 0.25-1.5 mm. wide, 3-3.5 mm. long, in fruit, 0.5-3.5 mm. wide, 4-7 mm. long, glandular and hirsutulous, narrowly oblanceolate-spatulate to broadly obovate; corolla lavender to violet, open-campanulate, 6-7 mm. long, the lobes 3 mm. long, slightly crenulate, the tube with thin translucent areas behind the stamens; corolla-scales 1.5-2.5 mm. long, quadrate, the free edges of adjacent scales between stamens connate throughout their length, at base attached to the filaments; stamens exerted, 7 mm. long, filaments with retrorse triangular processes, anthers oval, about 0.6 mm. long; style and branches 6.5-8.5 mm. long, the branches 4.5-6.5 mm. long, the style with a few bristly hairs and glands near the base; ovary about 1 mm. long, the top long-pilose-hairy and glandular, ovules 4-8;

capsule 4 mm. long, ovate, acute below prominent apiculation, hirsutulous and glandular, the back of the valves somewhat sulcate; seeds 1.5-2 mm. long, narrowly ovate, coarsely pitted, brown.

Gravelly or sandy soil in the main forest belt of the mountains, Modoc Co. to Kern Co., California, 3000 to 7000 ft.

Although Brand recognized *P. Purpusii* as a distinct species, he referred the collections from the northern Sierra Nevada to *P. humilis* var. *calycosa* Gray which he also maintained. I have already given an account of the identity of Gray's variety (Howell, 1942, p. 162), the type of which came from Yosemite Valley and not from "near Mono Lake."

Phacelia Purpusii is very closely related to *P. grisea* but besides the distinct geographic distribution of the two there are a number of minor morphologic differences by which they may be distinguished. These are indicated in the discussion of *P. grisea*. From the distribution of the three related species, *P. Purpusii*, *P. grisea*, and *P. mohavensis*, it may be judged that their dispersal is intimately connected with the dispersal in California of the Sierran Transition forest.

Collections, all from California. Near Goose Lake, Modoc Co., *R. M. Austin* (UC); Stalker's, Shasta Co., *M. S. Baker* No. 333 (ND, type of *P. trichostemoides* Greene ms.; UC); Goose Valley, Shasta Co., *Eastwood* No. 941 (CAS, G.M., NY, US); Little Summit, Butte Co., *Heller* No. 11486 (CAS, DS, G.M., ND, NY, UC, US); Park Creek Road, Eldorado Co., *Robbins* No. 1164 (CAS); Sherlock's, Mariposa Co., *Condon* in 1898 (DS, G, UC, US); Yosemite Valley, Mariposa Co., *Bolander* No. 6384 (G, type of *P. humilis* var. *calycosa*; NY, UC, US); Sequoia Mills (i.e. Millwood), Fresno Co., *T. S. Brandegee* in 1892 (UC), *Eastwood* in 1893 (DS); Black Oak Point, Sequoia National Park, Tulare Co., *J. T. Howell* No. 3084 (CAS); open forests, Middle Tule River, 5,000 to 6,000 ft., Tulare Co., *Purpus* No. 5603 (UC, type of *P. Purpusii*; G.M., US); Greenhorn Mts., Kern Co., *Peirson* No. 10702 (CAS, DS, FP, G, UC); above Parson's Mill, Poso Creek Valley, Kern Co., *Dudley* No. 584 (DS).

19. PHACELIA GRISEA Gray, Proc. Amer. Acad. 12:80 (1877)

Root annual; stems erect, rather sparsely leafy, widely or substrictly branched generally above the base, 2-6 dm. tall, glandular-hirsute and hirsutulous with longer and shorter non-glandular hairs and capitate glands; leaves lanceolate to elliptic or broadly ovate, 1-3 cm. long, 0.5-2 cm. wide, glandular and hirsutulous or strigose with the hairs more or less appressed, acute or subacute at apex, cuneate at base, entire or dentate-lobed, petioles to 3 cm. long; racemes becoming elongate, to nearly 2 dm. long, generally densely flowered, rarely the flowers scattered in the lower part, pedicels 1-2 mm. long; sepals quite unequal in width, in flower 3-4 mm. long, 0.25-2.5 mm. wide, in fruit 6-8 mm. long, 0.5-3.5 mm. wide, linear-oblancoaleate or narrowly oblanceolate-spatulate to rotund-obovate, obtuse or acute, narrowed below to claw-like base, glandular and hirsute; corolla "nearly white," open-campanulate, 5-5.5 mm. long, the tube 3 mm. long with a thin translucent area behind each stamen; corolla-scales 1.5-2.5 mm. long, quadrate, the free edges of adjacent pairs connate, truncate at top, attached below to the base of the filaments; stamens exerted, 7-8 mm. long, the filaments not hairy, generally roughened with

numerous retrorse papillae or rarely nearly smooth, anthers about 0.6 mm. long; style and branches 5.9 mm. long, the branches 4.5 mm. long, the style hairy up to the branches; ovary ovate, about 1 mm. long, long-bristly-hairy and glandular, ovules 10-12; capsule broadly ovate, 4.5 mm. long, acute below the terminal apiculation, bristly-hairy and glandular, the back of the valves shallowly sulcate; seeds 1.5 mm. long, ovate, acute, brown, finely to coarsely pitted.

In gravelly soil of mountain slopes and flats, Santa Lucia Mts., Monterey and San Luis Obispo counties, California, 2500 to 3500 feet.

Phacelia grisea, *P. Purpusii*, and *P. mohavensis* form a closely related group that is to be allied, though distantly, to *P. Pringlei* and its relatives. In all these species the corollas are very thin, but in *P. grisea*, *P. Purpusii*, and *P. mohavensis*, the corolla is especially thin and translucent in definite areas behind each stamen.

Phacelia grisea is very near *P. Purpusii* and it might be better to regard them as varieties of the same species. There is a real difference, however, in the vestiture of the two, and the number of ovules has proved to be constantly greater in *P. grisea*. These characters, together with such minor differences as the smaller size of the paler corolla and the smaller size of the seeds in *P. grisea*, indicate entities, which, even aside from the important consideration of their distinctly separate geographic occurrence, should be accepted as species, at least until the rare *P. grisea* is better known.

Collections. Pine Mt. near San Simeon Bay, San Luis Obispo Co., *Palmer No. 381* (G. type; CAS,F,M,UC); Pt. Sur, Monterey Co., *T. S. Brandegee in 1888* (UC); open in chaparral, canyon of the Arroyo Seco River, 2,500 to 3,000 ft., Monterey Co., *J. T. Howell No. 5696* (CAS); Tassajara Hot Springs, Monterey Co., *Elmer No. 3211* (DS); dry shale of clear areas, 3 miles north of Escondido Forest Service Camp on truck trail to Arroyo Seco, 3000 ft., Monterey Co., *Wolf No. 11000* (CAS,F,G, NY,P, RSA,US). A specimen in Herb. Greene. (ND) collected by Hickman in "Monterey County" in 1888 is probably *P. grisea*.

20. PHACELIA MOHAVENSIS Gray, Syn. Fl. 2, pt. 1: 164 (1878)

P. mohavensis Gray var. *exilis* Gray, *ibid.*, 165.

Root annual; stems erect, simple or narrowly and generally few-branched above or rarely widely branched from the base, 0.5-3 dm. tall, hirsute or hirsutulous, somewhat glandular above; leaves linear to oblong-lanceolate or narrowly oblong, 1.4 cm. long including the short more or less winged petiole, 0.1-1 cm. wide, entire or coarsely few-toothed or lobed, hirsutulous and a little glandular or the pubescence subappressed, subacute at apex, cuneate at base, petiole 1 cm. long or less; racemes to 2 dm. long, the lower flowers generally distant, the upper rather crowded, pedicels 2.5 mm. long; calyx-divisions unequal, in flower 2-7 mm. long, 0.3-1 mm. wide, in fruit very unequal and variable, 4.5-15 mm. long, 0.5-2 (or even 3) mm. wide, linear to oblanceolate-spatulate, hirsutulous and glandular; corolla lavender, open-campanulate, 5-8 mm. long, tube to 4 mm. long, with a thin transparent area behind each stamen; corolla-scales 1.5-2 mm. long, narrowly quadrate, truncate above, attached to corolla by one edge, the free edges of adjacent pairs connivent, at

base more or less united to base of filaments and forming a shallow pocket; stamens included or exerted a little, 5-8 mm. long, filaments retrorsely roughened but not hairy, anthers about 0.6 mm. long; style and branches 5-8 mm. long, the branches 3.5-6.5 mm. long, the style hairy only near the base or even to the lower part of the branches; ovary 1 mm. long, long-hairy and glandular above, ovules (4-) 7-11; capsule oblongish to broadly ovate, 3-5 mm. long, acute to subobtuse, shortly to prominently beaked, glandular-pilose, the back of the valves sulcate; seeds 1.3-1.5 mm. long, elliptic-ovate, acutish, brown, rather coarsely pitted.

Sandy or gravelly soil of moist slopes and flats or along stream courses, from the southern Sierra Nevada, Tulare County, to the San Bernardino Mts., San Bernardino County, California, 4000 to 7500 ft.

For the most part *P. mohavensis* presents a rather uniform appearance throughout its range, the most divergent variant examined being represented by the type of the species which was collected on the Mohave River by Palmer. This form is a round-topped plant widely and freely branched from the base, and the stems especially near the base are hirsute with numerous long stiff hairs. In my study of the species this might have been interpreted as an aberrant robust individual except that it was collected by Parish at Burcham's Ranch on the Mojave River "at or near the type locality" (No. 4859, DS) and again by Parish "on the banks of the Mohave River" (No. 1846, F). So it would seem that the type of the species represents a local strain and one quite different in appearance from the usual form of *P. mohavensis* which is found in the San Bernardino Mts. and elsewhere and which typifies Gray's var. *exilis*. Since so little is known of the occurrence and genetic character of the variant which is typical *P. mohavensis*, it has seemed best for the present to treat var. *exilis* merely as "a slender erect form" as Gray eventually did (1880, p. 467).

Two of the more important fluctuating variations exhibited by the numerous specimens examined should be mentioned. Of especial interest is the fact that ovaries are sometimes only 4-ovulate, a reduction in ovule number that would align *P. mohavensis* with species of *Euphacelia* related to *P. humilis*. Determinations on specimens indicate that Parish, for one, came to determine as *P. mohavensis* the southern Californian plant which I recently described as *P. austromontana*, a species in which the ovaries are uniformly 4-ovulate. Collections of *P. mohavensis* in which at least some of the ovaries are 4-ovulate are: San Bernardino Mts., Parish No. 1070 (CAS), Chandler in 1897 (UC); San Gabriel Mts., Duran No. 3512 (CAS).

Another occasional variation to be noted is in the development of the fruiting calyx-divisions. Almost always there is more or less unequal development of the divisions with one becoming longer and broader than the others, but usually all are relatively slender. Occasionally, however, the divisions are much enlarged and even foliaceous, as for example, in one plant of Parish No. 1070 in Herb. Calif. Acad. Sci. The calyx-divisions in the type collection and in Parish No. 4859 (DS) are longer and broader than is usual in the species but the divisions can scarcely be described as foliaceous.

Collections, all from California. Long Meadow, Tulare Co., *Hall & Babcock No. 5111* (DS,UC); Piute Mt., Kern Co., *Purpus No. 5303* (G,M,UC,US); Greenhorn Mts., Kern Co., *Kirkwood No. 276* (CAS); Mt. Pinos, Ventura Co., *H. M. Hall No. 6410* (UC); Pine Flats region, San Gabriel Mts., Los Angeles Co., *Ewan No. 7339* (CAS); Sulphur Springs, San Gabriel Mts., Los Angeles Co., *Duran No. 3512* (CAS, DS,F,G,M,RSA,UC,WS); Waterman Ridge, San Gabriel Mts., Los Angeles Co., *Carter No. 232* (CAS); Mohave River, San Bernardino Co., *Palmer 387 in 1876* (G, type; F,M,UC,US); Saragosa Spring, Upper Holcomb Valley, San Bernardino Mts., San Bernardino Co., *Hilend No. 535, 552* (CAS); Bear Valley, San Bernardino Mts., San Bernardino Co., *Parry & Lemmon in 1876* (G, type of var. *exilis*), *Munz No. 5674* (P), *Parish No. 3772* (CAS,G,ND,UC,US); Baldwin Lake, San Bernardino Mts., San Bernardino Co., *M. Peirson in 1932* (CAS,FP).

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Miscellaneous Notes on Nomenclature of United States Trees

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Introduction

In an examination of the original citations of names for the new Check List of the Native and Naturalized Trees of the United States, various nomenclatorial and bibliographic notes on United States trees were recorded. Some changes in names used by the Forest Service are necessary under the latest International Rules of Botanical Nomenclature (Ed. 3. 152 p. 1935. Internatl. Cong. Bot. 6th, Amsterdam, Proc. 2 v. 1935-36.) Notes on nomenclature of *Carya*, *Quercus*, and miscellaneous species have been submitted in other articles.¹ In this article are four new combinations in *Cereus*, *Rhamnus*, and *Salix*, and a few miscellaneous notes in *Quercus*, *Ilex*, and *Rhus*. Names published in rare or seldom consulted publications of Trew, Duhamel, Linnaeus, Bartram, Audubon, and Torrey are discussed. There are also notes on *nomina subnuda*, the gender of generic names, the original spelling of scientific names, and on names by other authors published by Linnaeus.

New Combinations

Cereus aboriginum (Small) Little, comb. nov. SHELLMOUND APPLE-CACTUS
Harrisia aboriginum Small in Britton and Rose, Carnegie Inst. Wash. Pub. 248 (Cactaceae), 2:154. 1920.

¹ LITTLE, ELBERT L., Jr. Notes on the nomenclature of *Carya* Nutt. Amer. Midland Nat. 29:493-508. 1943.

LITTLE, ELBERT L., Jr. New names in *Quercus* and *Osmanthus*. Wash. Acad. Sci. Jour. 33: 8-11. 1943.

LITTLE, ELBERT L., Jr. Homonyms among names of trees and fossil plants. Wash. Acad. Sci. Jour. 33:130-135. 1943.

Cereus fragrans (Small) Little, comb. nov. FRAGRANT APPLE-CACTUS

Harrisia fragrans Small in Britton and Rose, Carnegie Inst. Wash. Pub. 248 (Cactaceae), 2: 149, fig. 216, pl. 19, figs. 1-2. 1920.

The species of *Harrisia* Britton (Torrey Bot. Club Bul. 35:561. 1909) are slender, erect or reclining shrubs or small trees. Two of the three species in Florida which become 15 to 20 feet tall may reach the size of small trees and will be included in the new Check List.

Britton and Rose in their monograph on Cactaceae recognized 124 genera, including a large number of new genera, many of which have not been distinguished by conservative workers. Vaupel (in Engler and Prantl, Natürl. Pflanzenfam. Ed 2, 21: 633. 1925) accepted only 26 genera of Cactaceae and regarded *Harrisia* Britton as a synonym of *Cereus* Mill. (Gard. Dict. Abridged. Ed. 4, 1. 1754). It seems best to follow this conservative treatment for the small number of tree cacti in the United States and to transfer the two specific names to *Cereus*. The native tree cacti segregated under *Carnegiea* Britton and Rose, *Lemaireocereus* Britton and Rose, and *Lophocereus* Britton and Rose have been included under *Cereus*.

Rhamnus crocea var. **pirifolia** (Greene) Little, comb. nov.

GREAT REDBERRY BUCKTHORN

Rhamnus insularis Greene, Calif. Acad. Sci. Bul. 2: 392. 1877; in part.

Rhamnus crocea var. *insularis* Sarg., Gard. and Forest 2: 364. 1889; in part. Not *R. insulus* Kellogg, Calif. Acad. Sci. Proc. 2: 20. 1863. Not *R. crocea* subsp. *insula* (Kellogg) C. B. Wolf, Rancho Santa Ana Bot. Gard. Monog., Bot. Ser., 1: 36, fig. 10. 1938.

Rhamnus pirifolia Greene, Pittonia 3: 15. 1896.

Rhamnus crocea subsp. *pirifolia* (Greene) C. B. Wolf, Rancho Santa Ana Bot. Gard. Monog., Bot. Ser., 1: 45, figs. 4-c, 13-16. 1938.

The nomenclature of this variety has been discussed by Wolf. Here Wolf's subspecific name is merely transferred to a variety, in order that the nomenclature of categories below the rank of species be consistent. In the new Check List, varieties are maintained in preference to subspecies. Modern usage generally favors the category variety, which is so well established. Any attempt to introduce a new category for the variety and to transfer varietal names of the trees of the United States to subspecies would not clarify relationships of the trees but would cause unnecessary confusion in nomenclature.

Salix lasiandra var. **macrophylla** (Anderss.) Little, comb. nov.

Salix lucida macrophylla Anderss., Svenska Vetensk. Akad. Handl. 6:32. 1867.

Salix lucida β *macrophylla* Anderss. in DC., Prodr. 16(2):205. 1868.

Salix lasiandra var. *lyallii* Sarg., Gard. and Forest 8:463. 1895.

Salix lyallii (Sarg.) Heller, Torrey Bot. Club Bul. 25:580. 1898.

Salix lasiandra var. *lyallii* Sarg. was published as a new name based upon *Salix lancifolia* Anderss., Svenska Vetensk. Akad. Handl. 6:34, pl. 2, fig. 23. 1867. and *Salix lucida* β *macrophylla* DC. Sargent's explanation for the new name was that this specific and varietal name had been previously used. Both these names were cited as synonyms also, when the following earlier combina-

tion was made: *Salix lasiandra* var. *lancifolia* (Anderss.) Bebb in S. Wats., Bot. Calif. 2:84. 1879.

Sargent cited no specimen but referred to "a large-leaved form of *Salix lasiandra* discovered by Dr. David Lyall in 1859 on the lower Fraser River." *Salix lucida* β *macrophylla* Anderss. was based upon "lower Fraser-river" 49° lat. bor. (Dr. Lyall, 1859) et in ripis ad Rio River (Bourgeau, 1859)."

In making the new varietal name, Sargent was following an American Code rule which prohibited using the same epithet more than once in a genus, whether for a species or a variety. Article 29 of the International Rules permits use of the same epithet for subdivisions of different species within a genus. Thus, Sargent's varietal name is invalid as a synonym.

Miscellaneous Notes

x *QUERCUS BERNARDIENSIS* W. Wolf

Quercus alba \times *stellata*

\times *Quercus fernowii* Trel., Amer. Phil. Soc. Proc. 56: 49. 1917; *nomen nudum*.

\times *Quercus bernardiensis* W. Wolf, Torreya 18: 161. 1918.

\times *Quercus fernowii* Trel., Natl. Acad. Sci. Mem. 20: 15. 1924.

The binomials of hybrids of *Quercus* published by Trelease in 1917 (Naming American hybrid oaks. Amer. Phil. Soc. Proc. 56:44-52, illus. 1917) were nearly all *nomina nuda*, as only the supposed parent species were mentioned without description or reference to earlier descriptions. Under Article 31 the name of a hybrid is subject to the same rules as names of species and therefore requires a description (Articles 37 and 44).

Trelease's binomials of hybrids of 1917 were validly published in 1924 (The American oaks. Natl. Acad. Sci. Mem. 20, 255 p., illus. 1924). However, a few hybrids were named independently during this interval. Thus, \times *Quercus fernowii* Trel. must be replaced by \times *Quercus bernardiensis* W. Wolf.

In a similar case, the homonym *Quercus ashei* Sterrett (1922) invalidated \times *Quercus ashei* Trel. (1917, as *nomen nudum*; 1924). The latter was re-named \times *Quercus asheana* Little (Wash. Acad. Sci. Jour. 33: 8. 1943).

One of these binomials, \times *Quercus beadleii* Trel. (Amer. Phil. Soc. Proc. 56:48. 1917; *nomen nudum*), representing the cross between *Q. alba* and *Q. prinus*, apparently remains a *nomen nudum* without a published description.

ILEX AMBIGUA (Michx.) Torr.

CAROLINA HOLLY

Cassine caroliniana Walt., Fl. Carol. 242. 1788.

Prinos ambiguus Michx., Fl. Bor.-Amer. 2:236. 1803.

Ilex ambigua (Michx.) Torr., Fl. N.Y. 2: 2. 1843; as "ambiguus"; as to new combination but not description.

Ilex ambigua Chapm., Fl. South. U. S. 269. 1860.

Ilex caroliniana (Walt.) Trel., Acad. Sci. St. Louis, Trans. 5:347. 1889; *nomen provisorium*. Not *Ilex caroliniana* Mill., Gard. Ed. 8, *Ilex* No. 3. 1768.

The nomenclature of this species has been discussed by Rehder (Arnold Arboretum Jour. 3:214. 1922) and by Fernald (Rhodora 41:425-426. 1939), both of whom accepted the name *Ilex caroliniana* (Walt.) Trel. However, that name was invalidated in 1930 as a later homonym (Articles 60 and 61).

Small (Man. Southeast. Fl. 815. 1933) noted the earlier homonym and adopted *Ilex ambigua* (Michx.) Chapm. However, Chapman did not cite Michaux. Fernald (p. 428) referred *Ilex ambigua* sensu Torr. (1843) to *Ilex montana* Torr. and Gray. Under Article 54 *Ilex ambigua* (Michx.) Torr. as a new combination is the same as *Prinos ambiguus* Michx.

ILEX MONTANA var. *BEADLEI* (Ashe) Fern.

Ilex beadleii Ashe, Bot. Gaz. 24:377. 1897; *nomen subnudum*.

Ilex beadleii Ashe ex Kearney, Torrey Bot. Club Bul. 24:569. 1897.

Ilex dubia f. *beadleii* (Ashe) Loes., Nova Acta Acad. C. L. C. G. Nat. Cur. 78:487. 1901.

Ilex montana var. *beadleii* (Ashe) Fern., Rhodora 41:428. 1939.

The place of publication of the epithet of this variety of shrubs is not as generally cited: *Ilex beadleii* Ashe was originally published as scarcely more than a *nomen nudum*, though the geographic distribution was given. The vague synonymy upon which this new name was proposed is quoted here:

"*Ilex Beadleii*, nom nov. *Ilex mollis* of southern authors, and in part that of Gray's Manual. *Prinos dubius* Don is usually given as a synonym for this species, but the original description will scarcely apply to *I. Beadleii*, and the distribution assigned to *Prinos dubius*, from North Carolina to New Jersey, barely even extends as far south as the most northern point where *I. Beadleii* is known to occur. . . ."

This name apparently was not validated by the Gray Herbarium Card-index, which cited the synonymy merely as "*I. mollis* of southern authors, non A. Gray." Fortunately for stability in nomenclature, however, Ashe's name was promptly taken up the same year by Kearney who supplied a description, noting that "Mr. Ashe rightly segregates this plant from *I. monticola mollis* (A. Gray) Britton, but does not point out the characters by which his species can readily be distinguished." Thus the name dates from its publication in Kearney's article. Loesener, in reducing the name to a form, cited the references of both Ashe and Kearney.

x *RHUS BOREALIS* Greene

Rhus glabra × *typhina*

Rhus americana Dippel, Handb. Laubholz. 2: 367. 1892, *nomen provisorium*. Not

Rhus americana (Nutt.) Sudw., Torrey Bot. Club Bul. 19:80. 1892 (March 9).

Rhus glabra × *typhina* Koehne, Deut. Dendrol. 359. 1893.

Rhus glabra var. *borealis* Britton, Man. Fl. North. States Canada 601. 1901.

Rhus borealis Greene, Wash. Acad. Sci. Proc. 8: 188. 1906.

Rhus sandbergii Greene, Wash. Acad. Sci. Proc. 8:187. 1906.

Rhus glabra var. *sandbergii* Vasey and Holzinger ex Greene, Wash. Acad. Sci. Proc. 8:187. 1906; as synonym.

Rhus gymnoclada Greene, Repert. Spec. Novarum Regni Veg. 5: 45. 1908.

Rhus pulvinata Greene, Repert. Spec. Novarum Regni Veg. 5: 45. 1908.

Rhus hirta × *glabra* Koehne ex Schneid., Illus. Handb. Laubholz. 2: 154. 1912; *nomen nudum*.

Rhus hybrida Rehd., Deut. Dendrol. Gesell. Mitt. 22:256. 1913.

According to Rehder (Deut. Dendrol. Gesell. Mitt. 22:256. 1913), the first mention of a hybrid between *Rhus glabra* L. and *Rhus typhina* Torner as such was by Watson and Coulter (Gray, Asa. Man. Bot. North U. S. Ed. 6.

119. 1889). They stated briefly under *Rhus typhina* L.: "Apparently hybridizes with the next [*Rhus glabra* L.]." Koehne (Deut. Dendrol. 359. 1893) was the first to designate the hybrid by name. Britton and Brown (Illus. Fl. N. States Canada Ed. 2, 2:482. 1913) noted that *Rhus glabra* var. *borealis* Britton "may be a hybrid with *Rhus hirta*." However, Rehder (Deut. Dendrol. Gesell. Mitt. 22:256. 1913), in proposing the name *Rhus hybrida* Rehd. for the hybrid between *Rhus glabra* L. and *Rhus typhina* Torner, regarded *Rhus glabra* var. *borealis* Britton as a geographic variety of *Rhus glabra* L. In his monographic study of *Rhus*, Barkley (Mo. Bot. Gard. Ann. 24:265-498, illus. 1937) took up as a species rather than a hybrid the older name *Rhus pulvinata* Greene, with *Rhus hybrida* Rehd. as a synonym. He retained *Rhus glabra* var. *borealis* Britton also.

Later, Barkley (Amer. Midland Nat. 19:598-600, illus. 1938) reported the collection by C. C. Deam near Angola, Steuben County, Indiana, in September 1937 of *Rhus glabra* L., *Rhus typhina* Torner, *Rhus pulvinata* Greene, and *Rhus glabra* var. *borealis* Britton, all growing together. He concluded that *Rhus pulvinata* Greene and *Rhus glabra* var. *borealis* Britton probably were two groups of hybrid origin between the two species and suggested designation \times *Rhus pulvinata* Greene.

Under Article 34 of the International Rules different hybrid forms of the same parentage may be united under the binary name of the hybrid and may be classed like the subdivisions of a species. It seems desirable to designate these two groups of hybrids by a single binomial. The oldest available names are two species published simultaneously, *Rhus borealis* Greene and *Rhus sandbergii* Greene. Of these, the binomial \times *Rhus borealis* Greene, representing the variation usually known as *Rhus glabra* var. *borealis* Britton, is selected to include all hybrids between *Rhus glabra* L. and *Rhus typhina* Torner. As Greene did not cite Britton's older varietal name, *Rhus borealis* Greene stands as a new name, rather than a new combination. Greene remarked: "Although pubescent, this bears no relation to *R. hirta*." The type of \times *Rhus borealis* Greene was designated by Greene as a specimen collected by Charles A. Davis near Alma, Mich., Aug. 12, 1895, and deposited in the Herbarium of the Field Museum.

RHUS TYPHINA Torner

STAGHORN SUMAC

Datisca hirta L., Sp. Pl. 1037. 1753.

Rhus typhina Torner in L. and Torner, Cent. Pl. 2: 14. 1756; as "typhinum."

Rhus hirta (L.) Sudw., Torrey Bot. Club Bul. 19: 81. 1892. Not *Rhus hirta* Harv. ex Engler in DC., Phaner. 4:425. 1883; as synonym.

Britton (Torrey Bot. Club Bul. 18:269. 1891) noted that the oldest specific name associated with the staghorn sumac was *Datisca hirta* L. He stated: "The type of *Datisca hirta* preserved in the Linnaean Herbarium is a specimen of the Stag-horn Sumach in the condition of the inflorescence reverting to leaves, a phenomenon which frequently occurs in this and related species. Linnaeus had the plant from Kalm, and it was collected at Philadelphia." Sudworth (Torrey Bot. Club Bul. 19:81. 1892) made the combination *Rhus hirta* (L.) Sudw., which was later taken up by Britton, Rydberg, and Small.

Linnaeus's epithet "*hirta*" of 1753 has priority of three years over *Rhus typhina* Torner. Under Article 40 the combination *Rhus hirta* (L.) Sudw. is not invalidated by the earlier name, *Rhus hirta* Harv., published in synonymy. However, the name *Datisca hirta* L. should be rejected under Article 65, as it is based upon a monstrosity, with the inflorescence replaced by leaves. Thus, the name *Rhus typhina* Torner is valid for the staghorn sumac. Barkley (Mo. Bot. Gard. Ann. 24:326. 1937) has properly taken up Torner as the author of this species.

Generic Names Published by Trew, Herbarium Blackwellianum

Various pre-Linnaean generic names not accepted by Linnaeus in 1753 and 1754 were validly published within a few years in books which did not use binomials. Genera in these works are accepted by most modern authors, though Article 67 (3) and Example (2) raise some question about names of this kind. A number of these pre-Linnaean names were published by Miller (Gard. Dict. Abridged. Ed. 4, 3 v., illus. 1754) and restored by Druce (Bot. Exch. Club Sec. Brit. Isles Sup. 1913: 426-436. 1914). In most cases a change in citation to an earlier author of the same name is all that is necessary. However, a few of these obscure early names are homonyms or synonyms affecting well established names. In another article I have suggested that the names already in use be made *nomina conservanda*.

These three generic names in Lauraceae, among others, apparently date from Trew (Herbarium Blackwellianum. Centuria I-VI, illus. Norimbergae. 1750-1773). Nieuwland (Amer. Midland Nat. 1:221-224. 1910) called attention to *Sassafras* Trew (1757) and other names published in this work, and Louis C. Wheeler also has brought to my notice this generic name of Trew. These names, with the later places of publication usually cited are:

- Sassafras* Trew, Herb. Blackw., Cent. 3, pl. 267. 1757.
Sassafras Nees and Eberm., Handb. Med.-Pharm. Bot. 2:418. 1831.
Cinnamomum Trew, Herb. Blackw., Cent. 4, pl. 354. 1760.
Cinnamomum Blume, Bijdr. Fl. Ned. Indië 568. 1825.
Camphora Trew, Herb. Blackw., Cent. 4, pl. 347. 1760.
Camphora Nees in Wall., pl. As. Rar. 2:61. 1831.

Names appearing twice in 1754 are:

- Abies* Mill., Gard. Dict. Abridged. Ed. 4, v. 1. 1754. Not *Abies* Trew, Herb. Blackw., Cent. 2, pl. 198. 1754. I am suggesting that the former name be conserved.
Acacia Mill., Gard. Dict. Abridged. Ed. 4, v. 1. 1754. *Acacia* Trew, Pl. Select. pl. 36. 1754.
Cereus Mill., Gard. Dict. Abridged. Ed. 4, v. 1. 1754. *Cereus* Trew, Pl. Select. pl. 31. 1754.
Malus Mill., Gard. Dict. Abridged. Ed. 4, v. 2. 1754.
Malus Trew, Pl. Blackw., Cent. 2, pl. 141. 1754.

Generic Names Published by Duhamel, 1755

A few pre-Linnaean generic names of woody plants date from Duhamel *Traité Arbr. Arbust.* 2 v., illus. 1755) rather than from later authors, as usually cited. They include:

- Symphoricarpos* Duhamel, *Traité Arbr. Arbust.* 2: 295, pl. 82 and fig. 1755.

Laurocerasus Duhamel, *Traité Arbr. Arbust.* 1: 345, pl. 133 and fig. 1755; as "*Laurocerasus*."

Chamaecerasus Duhamel, *Traité Arbr. Arbust.* 1: 153, pl. 59 and fig. 1755.

G. N. Jones (*Arnold Arboretum Jour.* 21:203, 1940) in his monograph of the shrubby genus *Symphoricarpos* cited Duhamel as author. *Laurocerasus* Duhamel is generally suppressed as a synonym of *Prunus* L. Nieuwland (*Amer. Midland Nat.* 1:221-224, 1910), in calling attention to Duhamel's early work, mentioned *Laurocerasus* Duhamel and an earlier publication of the name in 1754 in a list of plants said to have been by Dom. Robbe. That rare publication has not been available to me. *Chamaecerasus* Duhamel is now treated as a subgenus of *Lonicera* L.

Cedrus Duhamel (*Traité Arbr. Arbust.* 1:139, pl. 52, and fig. 1755) is an earlier homonym of *Cedrus* Trew (*Cedr. Lib. Hist.* 6, illus. 1757). As *Cedrus* Duhamel is a segregate of *Juniperus* L., I am suggesting elsewhere that *Cedrus* Trew should be made a *nomen conservandum*.

Butneria Duhamel (*Traité Arbr. Arbust.* 1:113, pl. 45 and fig. 1755) was taken up by Kearney (*Torrey Bot. Club Bul.* 21:173-175, 1894) but now is one of three earlier homonyms of *Calycanthus* L. (*Syst. Nat.* 2:1066, 1371, 1759), *nomen conservandum*.

Uva-ursi Duhamel (*Traité Arbr. Arbust.* 2:371, illus. 1755) is an earlier homonym of *Arctostaphylos* Adans. (*Fam. Pl.* 2:165, 1763). The pre-Linnaean genus *Uva Ursi* Tourn. (*Elem. Bot.* 1:472, pl. 370, 1694) was published after 1753 as *Uva Ursi* Mill. (*Gard. Dict., Abridged. Ed.* 4, v. 3, 1754), two words, and as *Uva-ursi* Duhamel (1755), with a hyphen. Miller's name must be rejected under Article 67 (4) and is given as Example (4) of a rejected name originally published as two separate words not joined by a hyphen. Though Duhamel took up Tournefort's name (and drawings also) independently without citing Miller, *Uva-ursi* Duhamel was invalidated by the earlier *Uva Ursi* Mill.

New Genera in Linnaeus's *Systema Naturae*. Ed. 10, 1759

The new genera published in Linnaeus's *Systema Naturae* (Ed. 10, 2, 1759) appeared in two places in the text, though usually only the first and much briefer description is cited. The genera added by Linnaeus in this work, along with their species, were inserted in the text in proper order but without number. These added generic names were described in detail by number on pages 1359 to 1381, with cross references to the pages in the text where the species were inserted, but the volume had no index. The list, "Genera plantarum nova addenda," on pages 1357 and 1358 contained these 99 genera. Most were not new here, but were adopted from the works of P. Browne (*Civ. Nat. Hist. Jamaica.* 503 p., illus. 1756) and Loeffling (*Iter Hisp.* 1758), both published after Linnaeus's *Species Plantarum* (1753) and his *Genera Plantarum* (Ed. 5, 1754). Among the new genera were a few published by Linnaeus with other persons as author, such as *Halesia* Ellis (p. 1044, 1369). For accuracy both pages should be cited for these generic names. Linnaeus's book ended with eight genera with characters emended (p. 1358, 1381-1384).

In several of the new generic names, Linnaeus deliberately changed P. Browne's names but clearly cited the earlier names as synonyms. As a result, Linnaeus's names became established with his binomial nomenclature and had to be made *nomina conservanda* later. *Bucida* L. (p. 1025, 1368) and *Rhacoma* L. (p. 896, 1114) are established in usage and were in the 1927 Check List but are illegitimate under Articles 16 and 60 (1) as absolute synonyms. *Halesia* Ellis (p. 1044, 1369), also in usage and in the 1927 Check List, is a later homonym of *Halesia* P. Br. and *Halesia* Loeffl. These three generic names of Linnaeus are being retained in the new Check List, and I am including them in another article as names to be proposed as *nomina conservanda*. Other generic names in the Check List published by Linnaeus in 1759 are: *Lagerstromia* L. (p. 1076, 1372); *Piscidia* L. (p. 1155, 1364), *nomen conservandum*; and *Psychotria* L. (p. 929, 1364), *nomen conservandum*.

The generic names in Linnaeus's *Species Plantarum*, Ed. 1 (1753), are to be associated with the first subsequent descriptions under those names in Linnaeus's *Genera Plantarum*, Ed. 5 (1754) (Articles 20 and 42). Only one genus among those checked was found in one of these complementary works but not the other. It is: *Genipa* L. (Gen. Pl. Ed. 5, 87, 1754), first published in 1735. Though this genus was omitted in 1753, in 1759 Linnaeus published a species in it, *Genipa americana* L. (Syst. Nat. Ed. 10, 2:931, 1759).

Bartram's Catalogue

A few new species by Humphry Marshall in his *Arbustrum Americanum* (1785) were credited to "Bartram's Catalogue" and probably should be cited with Bartram as author. At the end of the introduction of his book, Marshall (p. xx) explained:

"The Reader is requested to observe that the names of the Species, under which the words, Bartram's Catalogue immediately occur, are not found in Linnaeus's *Species Plantarum*, but are taken from a Sheet Catalogue published by John and William Bartram, Botanists in Kingsessing; containing the names of Forest Trees and Shrubs, growing in, or near their Garden."

I have examined a photographic copy of this broadside Bartram's Catalogue in the Library of the Department of Agriculture. The original is among the rare collections in the Library of Congress and has not been available. This catalogue is a large broadsheet 21 by 17 inches. It is entitled: "CATALOGUE of AMERICAN TREES, SHRUBS and HERBACIOUS PLANTS, most of which are now Growing, and produce Ripe Seed in JOHN BARTRAM'S Garden, near Philadelphia. The Seed and growing Plants of which are disposed of on the most reasonable Terms." The bookshop selling the original and photographic facsimiles of this sheet stated in its typed description:

"No other copy of this very interesting and historical Sheet, the existence of which appears to have been known solely through a footnote reference made to it in Humphry Marshall's *Arbustrum Americanum*, appears to exist. Strangely enough, this is the copy owned and used by Humphry Marshall himself and contains his manuscript marginal additions and corrections. . . . It is not dated, but from an entry regarding 'undescript shrubs lately from Florida,' and the character and the type, it was probably printed in Phila. about 1790, possibly two or three years earlier. . . ."

The sheet catalogue consists of three double columns of names, with the Latin and English names in parallel columns, followed by a letter of reference indicating the kind of soil. Approximately 220 species are listed. Most have Latin generic and specific names, but a few have only the genus, and a few have longer Latin names. Specific names are capitalized, and a few have no English name. The new names were not indicated and were *nomina nuda*.

This may be the undated broadside cited by Barnhart (Bartonia 12, Sup., 66-67. 1931). He stated that trade catalogues were issued for many years and listed also four later catalogues dated 1807, 1814, 1828, and 1836. There is a photographic copy of the thirty-three page catalogue of 1807 in the Library of the Department of Agriculture.

As this copy of the broadside catalogue contains Marshall's marginal additions and corrections in ink and as at least one of the "undescript shrubs" was described by Marshall, it is probable that this is the "Bartram Catalogue" cited by Marshall in his book. Thus, the broadside catalogue can be dated as not later than 1785.

The names now accepted which were published by Marshall but credited to Bartram's Catalogue are:

- Franklinia* Bartram ex Marsh., Arbustr. Amer. 48. 1785.
Franklinia alatamaha Bartram ex Marsh., Arbustr. Amer. 49. 1785.
Lonicera canadensis Bartram ex Marsh., Arbustr. Amer. 81. 1785.
Nyssa ogeche Bartram ex Marsh., Arbustr. Amer. 97. 1785.
Populus deltoide Bartram ex Marsh., Arbustr. Amer. 106. 1785.

It may be assumed that the author of these names was William Bartram. At least, Marshall stated (p. 49) that the name *Franklinia* was chosen by William Bartram, who first introduced this species. In Bartram's Catalogue the name "*Alatamaha*" but not *Franklinia* appeared as one of "Three Undescript Shrubs lately from Florida."

The following names of trees now accepted and published by Marshall were also in the broadside catalogue, though Marshall did not cite it: *Betula papyrifera*, *Betula populifolia*, *Betula-Alnus maritima* (*Alnus maritima*), *Aesculus octandra*, *Fraxinus nigra*, *Nyssa sylvatica*, and *Vaccinium arboreum*.

In Bartram's Catalogue the printed spelling was "*Populus Delloidea*." The second "l" has been crossed by a pen to make a "t," the word has a wavy ink underscore, and after it is written in ink, "Delloide." In two other words, "Ilea" and "Cellis," the printed "l" was corrected to "t" with a pen. Thus it would appear that Bartram's spelling was "*deltoidea*" and that Marshall changed the spelling to "*deltoide*." Sargent (Silva No. Amer. 9:179. 1896) changed the spelling to "*deltoidea*." The present corrected spelling "*deltoides*" apparently dates from Sudworth (Torrey Bot. Club Bul. 20:44. 1893), who restored the name and noted that Koch (Dendrol. 2(1):487. 1872) had corrected the name to "*deltoides*" while regarding it as a doubtful synonym of *P. grandidentata*.

Audubon, Birds of America

The names of two species of forest trees of the United States first appeared in the famous, rare, elephant folio of John James Audubon's Birds of Amer-

ica, which contained colored plates without text. There these names were published as *nomina nuda* in legends of colored plates of birds. The twigs of the trees on which the birds illustrated were perched were well drawn. Their identity is clear, but no descriptions or "figure with analyses showing essential characters" (Article 44) were included. The citations, including the earliest known publications of the descriptions, are given below.

PLATANUS RACEMOSA Nutt.

CALIFORNIA SYCAMORE

California plane (horticulture)

Platanus racemosa Nutt. ex Audubon, Birds Amer. 4, pl. 362. 1837; as "*racemosus*"; *nomen nudum*.

Platanus racemosus Nutt., No. Amer. Sylva 1: 47, pl. 15. 1842; as "*racemosus*."

CORNUS NUTTALLI Audubon

PACIFIC DOGWOOD

Cornus nuttalli Audubon, Birds Amer. 4, pl. 367. 1837; *nomen nudum*.

Cornus nuttalli Audubon, Ornith. Biogr. 4: 482. 1838.

The place of publication of *Platanus racemosa* Nutt. was correctly given in Index Kewensis, a later publication generally cited for *Cornus nuttalli*, though the citation here was used by Jepson (Fl. Calif. 2:680. 1936).

The Abstract of Torrey's *Plantae Fremontianae*

A few names of shrubs and herbs apparently were first published in the following, generally overlooked, abstract: Torrey, John. On some new plants discovered by Col. Frémont, in California. Amer. Assoc. Adv. Sci. Proc. 4:190-193. 1851. This abstract of a paper read at the August 1850 meeting of the American Association for the Advancement of Science contains names of ten genera of California plants discovered by Frémont. Part of the names are *nomina nuda* or *nomina subnuda* and part had been published previously, but the following perhaps were described sufficiently to be accepted in the abstract: *Spraguea* (p. 191), *Coleogyne* (p. 192), *Emplectocladus* and *Emplectocladus fasciculatus* (p. 192), *Carpenteria* (p. 192), and *Sarcodes* and *Sarcodes sanguinea* (p. 193).

The fuller article, which is usually cited for these names, is: Torrey, John. *Plantae Frémontianae*; or, descriptions of plants collected by Col. J. C. Frémont in California. Smithsn. Inst. Contrib. Knowl. 5 (1) [6 (2)], 24 p., illus. 1853. The title page of this part recorded the date of publication as April 1853 (not 1854 as sometimes recorded), though the date of acceptance for publication was stated as September 1850. The Latin descriptions from this paper were quoted in the issue of *Flora* on Nov.-28, 1853 (*Flora* 36:704. 1853).

There was one substitution in the longer article. The abstract contained as a new genus and species *Darlingtonia rediviva* (p. 191), an "anomalous genus, apparently Bombaceous, . . ." Torrey dedicated "this fine new genus" to Dr. William Darlington, explaining that the old genus given to this botanist by De Candolle (*Darlingtonia* DC., Ann. Sci. Nat. 4:97. (1824) had been reduced to a section of *Desmanthus* by Benthham. This name was replaced in the longer article by the new species *Libocedrus decurrens*, which was not collected by Frémont.

Instead, Torrey assigned the name *Darlingtonia californica* to the California pitcher-plant, family Sarraceniaceae, in another publication of the series: Torrey, John. On the *Darlingtonia californica*, a new Pitcher Plant from northern California. *Smithsn. Contrib.* 6(5):1-8, pl. 12. 1853. It is regretted that the monotypic genus *Darlingtonia* Torr. (1853) has become invalid as a later homonym (Articles 60 and 61). The available name is *Chrysamphora californica* (Torr.) Greene (*Pittonia* 2:191. 1891). Perhaps *Darlingtonia* Torr. (1853) will be made a *nomen conservandum*, even though it has only one species.

Nomina Subnuda

Under Article 37, "A name of a taxonomic group is not validly published unless it is . . . (2) accompanied by a description of the group or by a reference to a previously and effectively published description of it." However, "description of the group" is not defined, and one is left to follow "established custom" (Article 5) for an interpretation of what constitutes the minimum description acceptable.

A new name published with no description at all and no reference to an earlier description clearly is rejected and is designated by custom as a *nomen nudum*, though that term does not appear in the rules. It is more difficult to decide whether names with very brief and indefinite descriptions are validly published under Article 37, or whether they should be rejected as *nomina subnuda*, or scarcely more than bare names. My own interpretation is to reject these inadequately described names, with due regard for the customs and knowledge of related plants at the time the names were published. Many *nomina nuda* can be identified with certainty, such as from herbarium specimens, later publications of the same author, through examination of the collector's itinerary, or by present knowledge of the geographical distribution of species. However, under the rules names to be valid must be based upon printed descriptions and not upon the searches of later workers, who may not always agree in their interpretations.

Article 4 states: "The essential points in nomenclature are: (1) to aim at fixity of names; (2) to avoid or to reject the use of forms and names which may cause error or ambiguity or throw science into confusion." Thus, there is definite authority for rejecting inadequately described names. The responsibility for publishing sufficiently described names rests entirely upon the publishing author. What counts is not what species the author meant, but what he published about it. Later authors are under no obligation to accept or account for names that are not clear. Names based upon mind-reading are insecure and sooner or later will be rejected by later workers with additional confusion. Some of these doubtfully described names were published incidentally in notes not intended as formal publication or were taken from field notes of the collector. It is contrary to Recommendation XV (e) to adopt unpublished names found in travelers' notes or herbaria, attributing them to their authors, unless these have approved publication.

There follow a few examples of names I regard as *nomina subnuda* and to be rejected under Articles 37, 5, and 4.

Juglans pecan Marsh. (Arbustr. Amer. 69. 1785), upon which the familiar name for the pecan, *Carya pecan* (Marsh.) Engl. and Graebn., was based, was published with a four line popular English discussion not acceptable as a botanical description. Accordingly, Marshall's name has been rejected by Rehder (Arnold Arboretum Jour. 22:571-572. 1941) and by Little (Amer. Midland Nat. 29:501-502. 1943). The accepted name for this species is *Carya illinoensis* (Wangenh.) K. Koch.

The name *Abies concolor* "J. L. and G. G." (Hort. Soc. London Jour. 5:210. 1850) first appeared in a list catalog of coniferous plants described only as "A tree" and with an unpublished name as a synonym. Yet, this citation appeared in Index Kewensis and was accepted by some authors, who may not have verified it. Thus, *Abies concolor* (Gord. and Glend.) Hoopes must date from the description of *Picea concolor* Gord. and Glend. (Pinetum 155. 1858).

Rafinesque's short, sketchy descriptions present some problems. It is doubtful whether later botanists are obliged under the rules to accept the names of Rafinesque based upon popular published descriptions of non-botanists, especially those of which Rafinesque did not see specimens or visit the localities where the plants grew. Illustrations of the names are those in his *Florula Ludoviciana* (179 p. 1817), taken from longer French descriptions by Robin, and those from Lewis and Clark. Asa Gray (Amer. Jour. Sci. 40:231-233. 1841) remarked that Rafinesque's new names in the *Florula Ludoviciana* "must be regarded as fictitious and unworthy of the slightest notice."

One example, *Sabal adiantum* Raf. (Fl. Ludov. 17. 1817) has been mentioned. Another, *Sambucus cerulea* Raf. (Alsogr. Amer. 48. 1838) was published as follows:

"*Samb. E. cerulea* Raf. frutex, fol. pinnatis, fl. cymosis, baccis pallide ceruleis—mentioned by Lewis and Clarke trav. 2. p. 160, as growing near Oregon Mts. must be better described; but the blue berries are quite peculiar."

On the preceding page Rafinesque wrote that he had seen alive all the American species of *Sambucus* and had them in his herbal except this one. (Incidentally, Rafinesque had been offered the position as botanist with the Lewis and Clark expedition but had declined it.)

Sudworth rejected this name in his first check list (U. S. Dept. Agr. Div. Forestry Bul. 14:338. 1897) but accepted it in his later check list (U. S. Dept. Agr. Misc. Circ. 92:235. 1927) as based upon the Lewis and Clark reference to an "alder" with pale "sky-blue" berries, the only elder in the Northwest fitting the description. Lewis and Clark also regarded it as the same as that of the East, which had berries "of a deep purple." Most recent authors have accepted Rafinesque's name in preference to *Sambucus glauca* Nutt. (ex Torr. and Gray, Fl. No. Amer. 2:13. 1841). However, St. John (Fl. Southeast. Wash. Adj. Idaho 394. 1937) in using Nuttall's name remarked: "*S. cerulea* Raf. is probably this plant but its description is inadequate. Rafinesque never saw it, naming it from a few non-technical words in the Lewis and Clark Travels. No specimen was preserved by the Lewis and Clark Expedition." I am adopting *Sambucus glauca* Nutt. and rejecting *Sambucus cerulea* Raf. also.

Rafinesque's earlier name doubtless is the same species but he did not publish an acceptable description.

Yucca schidigera Roezl (ex Ortgies, 20:110. 1871) is an illustration of a name apparently not intended as publication of a new name but was briefly mentioned by Ortgies in a German account of the travels and collections of Roezl. It was merely noted as one of two species of *Yucca* found near San Diego, California: arborescent, with short broad leaves edged with stout, pendent, loosely curled fibers and was named by Roezl *Y. schidigera* because it resembled *Agave schidigera*.

Trelease (Mo. Bot. Gard. Rpt. 13:113. 1902) placed *Yucca schidigera* Roezl as a synonym of the later name, *Yucca Mohavensis* Sarg. (Gard. and Forest 9:104. 1896) and Standley (U. S. Natl. Mus. Contrib. U. S. Natl. Herbarium 23:94. 1920) had the former a doubtful synonym. Macbride regarded Roezl's name as practically a *nomen nudum*. However, McKelvey (Yuccas Southwest. U. S. pt. 1:95-96. 1938) considered Ortgies brief description adequate because there are only two species of *Yucca* native near San Diego and his description was sufficient to separate them. She expressed regret at the change but felt obliged under the rules to adopt *Yucca schidigera* because there was no doubt as to the identity of the species, though none of Roezl's material was available.

Benson (Amer. Jour. Bot. 30:235. 1943) also accepted the name *Yucca schidigera* Roezl but Kearney and Peebles (U. S. Dept. Agr. Misc. Pub. No. 423 (Fl. Pl. Ferns Ariz.): 198. 1942) did not. I agree that the two names represent the same species but I agree also with Trelease, Standley, Macbride, and Kearney and Peebles in rejecting *Yucca schidigera* Roezl as invalidly published under the rules. *Yucca Mohavensis* Sarg. is properly published for this species and can be accepted without confusion.

Gender of Generic Names

Several generic names have been regarded by certain authors as having different genders. The rule for governing gender (Article 72) was modified in 1935. The gender of a few tree names is discussed here. Only two changes are noted from the usage by Sudworth in his 1927 Check List (U. S. Dept. Agr. Misc. Circ. 92, 295 p. 1927).

CHIONANTHUS L., Sp. Pl. 8. 1753; Gen. Pl. Ed. 5, 9. 1754.

Linnaeus assigned feminine gender to this genus with two species, and that gender was used for the single species in the 1927 Check List. According to Article 72 (2), names ending in *-anthos* or *-anthus* ought strictly to be neuter, since that is the gender of the Greek word *anthos*. However, this rule states further that these names have been with very few exceptions treated as masculine, hence it is agreed to assign that gender to them. Thus, the name is masculine and the species is *Chionanthus virginicus* L.

CONOCARPUS L., Sp. Pl. 176. 1753; Gen. Pl. Ed. 5, 81. 1754.

Linnaeus indicated that this monotypic genus was feminine, by using the

ending *Conocarpus erecta*, followed in the 1927 Check List. However, under Article 72 (2), all modern compounds ending in the Greek masculine *carpos* (or *carpus*) are masculine. Thus, this name is masculine and the specific name becomes *Conocarpus erectus* L.

PHYLLANTHUS L., Sp. Pl. 981. 1753; Gen. Pl. Ed. 5, 422. 1754.

This name, like *Chionanthus*, was treated by Linnaeus as feminine but is masculine under Article 72 (2) and in current publications.

RHAMNUS L., Sp. Pl. 193. 1753; Gen. Pl. Ed. 5, 89. 1754.

Linnaeus treated this name as masculine. However, the classical gender, feminine, is preferred under Article 72, Recommendation 1, adopted in 1935. In modern usage *Rhamnus* is uniformly treated as feminine.

RHUS L., Sp. Pl. 265. 1753; Gen. Pl. Ed. 5, 129. 1754.

This name has been treated as masculine, feminine, and neuter, though by uniform modern usage the gender is feminine. Of the 12 species of *Rhus* published simultaneously by Linnaeus in 1753, 2 had feminine endings, 3 had neuter endings, 1 was a participle, and 6 were nouns in apposition. Tournefort earlier had the name neuter. However, as *Rhus* is of classical Greek and Latin origin, the classical gender should be retained. The Greek gender was both masculine and feminine, according to Liddell and Scott (Greek-English Lexicon. Ed. 7, 1366. 1889), who stated that Dioscorides used the masculine form. Harper's Latin Dictionary (Rev. Ed. 1594. 1891) gave the Latin gender as masculine, but also feminine in one reference. The evidence from classical Greek and Latin favors masculine over feminine. However, trees are generally feminine in Latin and in modern scientific names. Article 72 (1), adopted as a recommendation in 1935, states that the author has the right of choice between the alternative genders where the classical gender varies and that in doubtful cases, general usage should be followed. Linnaeus used both the classical gender feminine and the non-classical gender neuter. Thus, the universally used feminine gender should be retained.

SABAL Adans., Fam. Pl. 2:495. 1763.

The question of the gender of *Sabal* was raised in 1917 in an unsigned note (Kew Roy. Bot. Gard. Bul. Misc. Inform. 1917: 212-213. 1917), which stated that good authors, including Index Kewensis, regarded it as neuter and other good authors as feminine. Adanson had no species in his genus and did not explain the origin of the name, which is thought to be an American Indian word. As the name was not of classical Greek or Latin origin, the gender is determined under Article 72 (3), which states that where the original author failed to indicate the gender, the next subsequent author has the right of choice.

The first specific epithet, which does not indicate the gender, was: *Sabal adansonii* Guersent (Soc. Philom. Paris Bul. des Sci. 3:206. 1803 [or

1804?]), a synonym of *S. minor* (Jacq.) Pers. The second specific name and first to show gender, as stated in the note on the gender of *Sabal*, was: *Sabal carolinianum* Hort. ex Poir. (in Lam., *Encycl. Méth. Bot.* 6:357. 1804). Though the gender was neuter the name was invalid and therefore could not establish the gender. *Sabal carolinianum* was a *nomen nudum* (Articles 37 and 44) and also published as a synonym of *Corypha minor* Jacq. (Article 40). As under Article 60, an illegitimate name must not be considered for purposes of priority, *Sabal carolinianum* must be passed over in determining the gender also.

The first name in which it can be said that the gender of *Sabal* was chosen was: "*Sabal ? adiantinum*. Raf." (Fl. Ludov. 17. 1817). The name had the characteristically short description of Rafinesque, six words of Latin and a reference to Robin's popular description. It is questionable whether Rafinesque's name was more than a *nomen subnudum* and not accompanied by adequate description for recognition (Articles 37 and 44). Moreover, as Asa Gray (*Amer. Jour. Sci.* 40:231-233. 1841) stated, there is sufficient cause for rejecting all names of doubtful identity in that more or less fictitious work, the new names of which were based upon popular French descriptions published by Robin. Rafinesque saw none of the plants and never did visit the State of Louisiana. Bailey (*Gentes Herbarum* 3:301. 1934) cited *Sabal adiantinum* Raf. as probably a synonym of *S. deeringiana* Small. Bomhard (*Wash. Acad. Sci. Jour.* 25:44. 1935) placed Rafinesque's name as a synonym of *Sabal louisiana* (Darby) Bomhard, based upon an earlier (1816) and also briefly described name for *S. deeringiana*. Thus, it is doubtful whether the gender of the genus was established by Rafinesque's name.

Next in priority was *Sabal pumila* Ell. (*Sketch Bot. S.-C. Ga.* 1:430. 1817; probably Dec.), a synonym of *S. minor* (Jacq.) Pers. Elliott's name appeared probably in December 1817, according to Barnhart (*Torrey Bot. Club Bul.* 28:687. 1901), the same year as Rafinesque's, not in 1821, the date on the title page of the volume. If *Sabal pumila* Ell. is accepted as the first legitimate name to show gender, then the gender of *Sabal* is feminine. In view of the uncertain status of Rafinesque's name, it seems best to retain the gender as feminine in accordance with modern authors in general.

STYRAX L., *Sp. P.* 444. 1753; *Gen. Pl. Ed.* 5, 203. 1754.

Styrax was designated by Linnaeus as neuter. Under the rules, the classical gender, feminine, which is in general use, is recommended.

Original Spelling of Scientific Names

Under the rules (Article 70), the original spelling of a name must be retained, except in the case of a typographical error, or of a clearly unintentional orthographic error. Sprague (*Kew Roy. Bot. Gard. Bul. Misc. Inform.* 1928: 349. 1928) has remarked and Moldenke (*Rev. Sudamer. de Bot.* 5:42. 1937) has repeated that "it is generally undesirable to 'correct' the original spelling, as different authors may 'correct' it in different ways."

In verifying the citations of tree names, I have been careful to note the original spelling and to restore the original spelling in the few cases where a changed spelling is in use. In the new check list, where it has been necessary to change the spelling, such as in restoring an original spelling changed by later authors or in changing the gender, the author's spelling has been added in quotations. Several miscellaneous notes on spelling of generic and specific names follow.

The less familiar original spelling of a few generic names has been restored. These names include:

ALBIZIA Durazz., Mag. Tosc 3 (4): 10, 13, illus. 1772. Not "Albizzia," as in general usage.

I have examined this very rare publication and find that the name was spelled uniformly (p. 10, 11, 13, and plate) "*Albizia*," though Durazzini stated that the name honored "Il Sig. Cavalier Filippo degl' Albizzi." In restoring this name, Bentham (Hook. London Jour. Bot. 3:84. 1844) stated that he preferred the spelling "*Albizzia*."

ANNONA L., Sp. Pl. 536. 1753; Gen. Pl. Ed. 5, 241. 1754.

Not "*Anona*," as in Sudworth's 1927 Check List.

JACQUINIA Sandmark in L. and Sandmark, Fl. Jamaicensis 27. 1759.

Not "*Jacquinia*," as adopted by Jacquin himself a year later (Enum. Pl. Carib. 2. 1760).

Sandmark's original spelling "*Jacquinia*," which was used by Sudworth in his 1927 Check List, should be maintained.

PITHECELLOBIUM Mart., Flora 20 (2), Beibl. 114. 1847; as "*Pithecollobium*;" *nomen conservandum*.

Pithecollobium Mart., Hort. Reg. Man. 188. 1829; *nomen nudum*.

This name is often spelled "*Pithecolobium*" and so appeared in the 1927 Check List. It was first published as "*Pithecellobium*," a *nomen nudum*, but was validly published as "*Pithecollobium*." When the name was conserved, the orthographically correct spelling "*Pithecellobium*" was adopted.

SIMAROUBA Aubl., Pl. Guiane Franc. 2:859, pl. 331-332. 1775.

Not "*Simaruba*," as changed by de Candolle (Paris Mus. d'Hist. Nat. Ann. 17:423. 1811).

Simarouba Aubl. used in the 1927 Check List, though some authors have adopted "*Simaruba*." Sprague (Kew Roy. Bot. Gard. Bul. Misc. Inform. 1929: 243. 1929) has explained that Aublet adopted the Carib name "*Simarouba*" for the genus and that that spelling must be retained.

ZANTHOXYLUM L., Sp. Pl. 270. 1753; Gen. Pl. Ed. 5, 130. 1754.

Not "*Xanthoxylum*," as used in the 1927 Check List, and many authors.

The variant and orthographically correct spelling *Xanthoxylum* L. corr. J. F. Gmel. (Syst. Nat. Ed. 13, 2:509. 1791) was proposed in 1935 as a *nomen genericum conservandum propositum* (International Rules. Ed. 3, 135. 1935). However, this proposal was not accepted by the 1935 congress.

ZIZIPHUS Mill., Gard. Dict. Abridged. Ed. 4, v. 3. 1754. Not "*Zizyphus*," as in usage.

Sprague (Kew Roy. Bot. Gard. Bul. Misc. Inform. 1929: 52. 1929) has noted that Miller's choice should be final.

One interesting original spelling that can be rejected as a typographical error (Article 70) is: *Canotia* Torr. (U. S. Rpts. Expl. Surv. Miss. Pacif. 4: 68. 1857). Apparently the "C" was lost in the type, as the original spelling was "*anotia*." The spelling "*anotia*" occurred in both editions (33rd Congr., 2d Sess., Senate Exec. Doc. No. 78. 33d Congr., 2d Sess., House Exec. Doc. No. 91.). Fortunately, the common name was given as "*Canotia*" and the spelling in the index (p. 171) was "*Canotia*."

The few generic names which Linnaeus spelled differently in his Species Plantarum (1753) and his Genera Plantarum (Ed. 5. 1754) have been spelled in accordance with Article 71. The names of this class in which the spelling of the new check list differs from that of Sudworth's 1927 Check List include:

Citharexylum L. (As "*Citharexylon*" in the 1927 Check List.)

Euonymus L. (As "*Evonymus*" in the 1927 Check List.)

Guaiaacum L. (As "*Guaajacum*" in the 1927 Check List.)

Other names spelled by Linnaeus in two ways in 1753 and 1754, but which remain unchanged are *Liriodendron*, *Rhododendron*, *Sideroxylon*, *Staphylea*, and *Thuja*.

Fernald (Rhodora 42:94-95. 1940) and Egler (Rhodora 43:220-222. 1941) have noted that the spellings "*pensylvanicus*" and "*pennsylvanicus*" were both used correctly under different species and that the original spelling should be preserved in each case. The following tree names may be noted:

Acer pensylvanicum L., Sp. Pl. 1055. 1753.

Crataegus pennsylvanica Ashe, Carnegie Mus. Ann. 1: 394. 1902.

Fraxinus pennsylvanica Marsh., Arbustr. Amer. 51. 1785.

Prunus pensylvanicus L. f., Sup. Pl. Ed. 13, 252. 1781.

In specific names honoring persons the original spelling of the second declension Latin genitive, whether "i" or "ii" must be retained. Much unnecessary effort is required to remember and use the correct spelling. Thus, there exist in the same genus:

Salix amygdaloides var. *wrightii* (Anderss.) Schneid., Bot. Gaz. 65:14. 1918.

Salix bonplandiana var. *toumeyii* (Britton) Schneid., Bot. Gaz. 65: 20. 1918.

Salix coulteri Anderss., Svenska Vetensk. Akad. Öfversigt af. . . Förhandl. 15: 119. 1858.

Salix discolor var. *overi* Ball, Rhodora 26: 137. 1924.

- × *Salix glatfelleri* Schneid., Arnold Arboretum Jour. 3: 79. 1922.
Salix gooddingi Ball, Bot. Gaz. 40: 376, pl. 12, figs. 1-2. 1905; usually spelled "gooddingii."
Salix harbisoni Schneid., Arnold Arboretum Jour. 1: 29. 1919.
Salix lasiandra var. *abramsi* Ball, Bot. Gaz. 72: 224. 1921.
Salix lasiandra var. *lyallii* Sarg., Gard. and Forest 8:463. 1895.
Salix lasiolepis var. *bigelovii* (Torr.) Bebb in S. Wats., Bot. Calif. 2: 86. 1879.
Salix lasiolepis var. *sandbergii* (Rydb.) Ball, Wash. Acad. Sci. Jour. 28: 448. 1938.
Salix longipes var. *wardi* (Bebb) Schneid., Bot. Gaz. 65: 22. 1918; as "wardii."
Salix lutea var. *watsoni* (Bebb) Jepson, Man. Fl. Pl. Calif. 266. 1923.
Salix nigra var. *lindheimeri* Schneid., Bot. Gaz. 65: 9. 1918.
Salix tracyi Ball, Calif. Univ., Pubs., Bot. 17:403, pls. 69-70. 1934.

Though the common spelling is *Picea engelmannii*, the Engelmann spruce should be known by the original spelling *Picea engelmanni* Parry (ex Engelm., Acad. Sci. St. Louis, Trans. 2:212. 1863).

Standardized Plant Names (Ed. 1, 1923. Ed. 2, 1942) had adopted the uniform single "i" for this genitive ending. It is hoped that the International Rules will be amended to adopt the same, simplified practice of uniform endings.

M. L. Green (Kew Roy. Bot. Gard. Bul. Misc. Inform. 1939: 325. 1939) proposed the following amendment as a note to be added to Article 70:

"Note 2 bis. The use of the terminations *i* or *ae* instead of *ii* and *iae*, prescribed in Rec. XL (b) and XLI, is treated as an unintentional orthographic error which may be corrected."

A simpler amendment would be a recommendation permitting the correction of the terminations *ii* to *i* and *iae* to *ae* in all cases and repealing the recommendations under which the endings vary according to the preceding letters.

It is hoped that botanists who like to restore the original spelling will not be interpreting Article 70 too rigidly. For example, the original spelling of *Cupressus macnabiana* A. Murr. (Edinb. New Phil. Jour., new ser., 1:293, pl. 11. 1855) was *M^cNabiana*. Some of the longer specific names published in the margins of Linnaeus's *Systema Naturae* (Ed. 10, 2. 1759) were shortened, possibly by the typesetter, ending abruptly when the line was filled, though others were hyphenated and continued on the second line. These abbreviated names offer no problems, as they were printed in full in the second edition of the *Species Plantarum* (1762-63) and are spelled in full in *Index Kewensis*. The abbreviated original spellings of trees in the check list include:

- Amyris balsamif.* L., Syst. Nat. Ed. 10, 2: 1000. 1759. Later changed to *A. balsamifera* L., Sp. Pl. Ed. 2. 496. 1762.
Amyris elemifer. L., Syst. Nat. Ed. 10, 2: 1000. 1759. Later changed to "*elemifera*."
Cedrela mahag. L., Syst. Nat. Ed. 10, 2: 940. 1759. Later changed to "*mahagoni*."
 Now *Swietenia mahagoni* Jacq.
Chrysophyllum olivifor. L., Syst. Nat. Ed. 10, 2:937. 1759. Later changed to "*oliviforme*."
Citharexylum fruticos. L., Syst. Nat. Ed. 10, 2: 115. 1759. Later changed to "*fruticosum*."
Conocarpus racemos. L., Syst. Nat. Ed. 10, 2: 930. 1759. Later changed to "*racemosus*."
 Now *Laguncularia racemosa* (L.) Gaertn. f.

Myrtus zuzygiu. L., Syst. Nat. Ed. 10, 2: 1056. 1759. Later changed to "zuzygium."
Now *Calyptanthus zuzygium* (L.) Sw.
Rhacoma crossopet. L., Syst. Nat. Ed. 10, 2: 896. 1759. Later changed to "*crossopetalum*."

Names by Other Authors Published by Linnaeus

A few names in Linnaeus's works were attributed to other authors and should be so cited, yet some modern references do not give credit. These include names suggested by Linnaeus's correspondents and in honor of other persons. Examples among the trees of the United States are:

Cyrilla Garden ex. L., Mant. Pl. 1: 5. 1767.
Halesia Ellis ex L., Syst. Nat. Ed. 10, 2: 1044, 1369. 1759.
Halesia carolina Ellis ex. L., Syst. Nat. Ed. 10, 2: 1044. 1759.
Hopea tinctoria Garden ex. L., Mant. Pl. 1: 105. 1767. Now, *Symplocos tinctoria* (Garden) L'Hérit.

Likewise, the new names published by Linnaeus's students in dissertations in the series, *Dissertationes Academicæ*, of the Royal Academy at Upsala, should be credited to the students as authors.

Illustrations are:

Jaquinia Sandmark in L. and Sandmark, *Fl. Jamaicensis* 27. 1759.
Rhus typhina Torner in L. and Torner, *Cent. Pl.* 2: 14. 1756; as "*typhinum*."

FOREST SERVICE,
U. S. DEPT. OF AGRICULTURE,
WASHINGTON, D. C.

Quercus Durandii and its Allies

Ernest J. Palmer

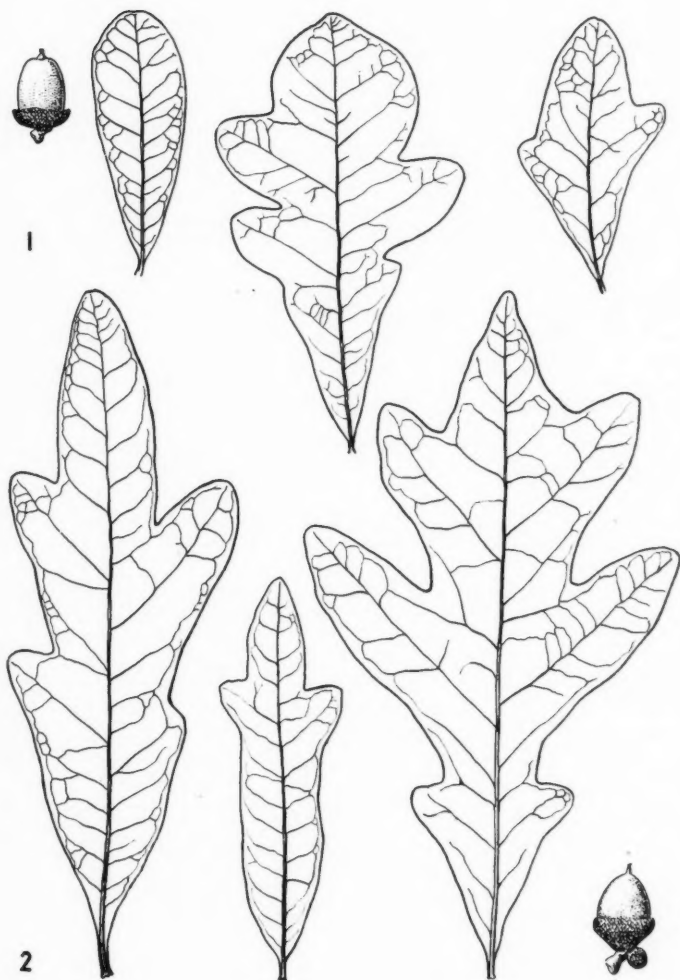
Quercus Durandii is a comparatively rare and little known white oak of the Gulf coastal plain. It is well marked and is easily distinguishable from most of the other oaks of the region, but two or three other related species have been described and there has been some confusion in the treatment of them. The whole group is calciphile and plants are usually found only in limestone regions or on marly soil.

Buckley's description¹ was clear and accurate. The range given by him was Wilcox County, Alabama, upper Louisiana and middle and southern Texas. He stated that it was called basket oak or bastard white oak and that the wood was often worked into splints for baskets to hold the picked cotton and that it was much sought after for screws for cotton gins. He published a second paper on it in 1881,² giving additional notes and localities and defending it as a distinct species. The typical form has since been found near Albany and Desoto, Georgia, and at a number of other stations in Alabama, Mississippi, Louisiana and Texas. From Louisiana it extends up the valley of Red River into southwestern Arkansas, and it has been reported from the vicinity of Dallas, Texas. In southern Texas it is found along or near the coast as far west as Victoria and Calhoun counties, and apparently locally along streams in the neighborhood of Austin and San Marcos, and in Milam County, as reported by Buckley. The stations where it is found are often widely separated and it is absent from wide intervening areas. From Louisiana I have seen specimens only from the vicinity of Shreveport and Natchitoches.

Quercus Durandii usually grows along streams or in fertile soil on low hills near the coast. It is a small or medium sized tree, seldom over 20 meters tall, with a clear trunk covered with thin, slightly scaly, pale or silvery gray bark, and with a symmetrical rounded or conical crown. The leaves are generally smaller than in any other arborescent white oak of the region, and they are extremely variable in shape and often asymmetrical. They are mostly oblong-elliptic to obovate in outline, entire or undulate on the margins, trilobate at apex or with additional low, rounded lateral lobes, mostly 3-10 cm. long, 1.5-3.5 cm. wide, or rarely larger and sometimes more deeply lobed on sterile shoots, cuneate or narrowed at base, rounded at apex, pubescent beneath when young, thin and glabrous on both sides at maturity and then bright or yellowish green and glossy above, sometimes green or often pale or silvery gray beneath. The fruit is ovoid or short cylindric, 1-1.5 cm. long, the nut 9-12 mm. thick, 1/5 or less enclosed in the thin, very shallow or almost disc-like cup, its scales pale brownish gray, pubescent and closely ap-

¹ Proc. Acad. Sci. Phila., 1860, 445. 1860.

² Proc. Acad. Sci. Phila. 1881, 121-122. 1881.

Fig. 1. *Quercus Durandii*.Fig. 2. *Quercus Durandii* var. *austrina*.

pressed. A hybrid with *Quercus stellata* has been found—*xQ. macnabiana* Sudw.³

In the same paper and in the next paragraph after the description of *Quercus Durandii* Buckley also described the shrubby oak, *Q. annulata*. He did not compare the two species, although the descriptions and more particularly an inspection of the plants in the field suggests their close relationship.

It has been found that the name *Quercus annulata* is untenable because of two earlier homonyms. But Sargent⁴ in 1895 had published the name *Quercus breviloba* for this plant, based upon *Q. obtusifolia breviloba* Torrey, and in his Silva⁵ he gave *Quercus Durandii* Buckl., *Q. annulata* Buckl. and *Q. san-sabeana* Buckl. (Buckley ex Young) as synonyms under that name. In later publications Sargent recognized *Quercus Durandii* as a distinct species, and the name *Quercus breviloba* was restricted by him and by other authors to the shrubby plant. There is some reason to doubt from Torrey's brief description and from the region where his material was collected whether his plant was really the same as *Quercus annulata* Buckl. But as the latter is here treated as a variety, it seems best to retain this familiar name, making it *Quercus Durandii* var. *breviloba* comb. nov.

Buckley described *Quercus annulata* as a shrub or small tree and he stated that it is common on the limestone hills in the vicinity of Austin, Texas. As a matter of fact it has a rather wide range through the Edwards Plateau of Texas as far west as Devils River and with a local extension northward into the Arbuckle Mountains of Oklahoma. It is often very abundant on limestone hills or in small canyons where it grows as a shrub 1-4 m. tall, or rarely in more protected situations or in richer soil it becomes a small tree up to 8-10 m., usually with a crooked trunk branching from near the base. The leaves of the two varieties are very similar in size and outline, although those of the variety *breviloba* are usually firmer in texture and more uniformly pale on the under surface, and the acorn cups are rounded, deeper and sometimes slightly thicker than in typical *Q. Durandii*. But in shade the leaves may occasionally be thinner and green beneath. Even as a tree, the habit of *breviloba* is different from that of the typical variety, but it is sometimes difficult to distinguish between them in sterile herbarium specimens.

The wide but interrupted distribution of *Quercus Durandii* and its comparative rarity and restriction to definite ecological areas suggest that it may be a relict species that was once more abundant under conditions more favorable to it. If this is the case, it is probable that the shrubby plant was developed as an ecological form adapting itself to a different and dryer habitat.

In the southeastern and central part of the coastal plain another tree is found that has sometimes been confused with *Quercus Durandii*. This was described by Small⁶ as *Quercus austrina*. It becomes a taller tree than *Q.*

3 U. S. Dept. Agric. Miscel. Circular 92, 103. 1927.

4 Gard., and Forest, 8:93. 1895.

5 Silva, 8:71. 1895.

6 Fl. Southeastern U. S. 353, 1329. 1903.

Durandii, attaining a maximum height of 25 m. or more. The bark of the two trees is similar and there is some resemblance in the leaves and fruit. But the leaves of *Q. austrina* average larger, are more regularly and deeply lobed, and are not silvery or white on the under surface. The cups of the acorns are rounded or slightly turbinate, enclosing about 1/3 of well-developed nuts. These differences are obvious and constant, but the general resemblance in habit and in the foliage and fruit of the two trees clearly indicates a close relationship and that they are probably only well-marked varieties of a single

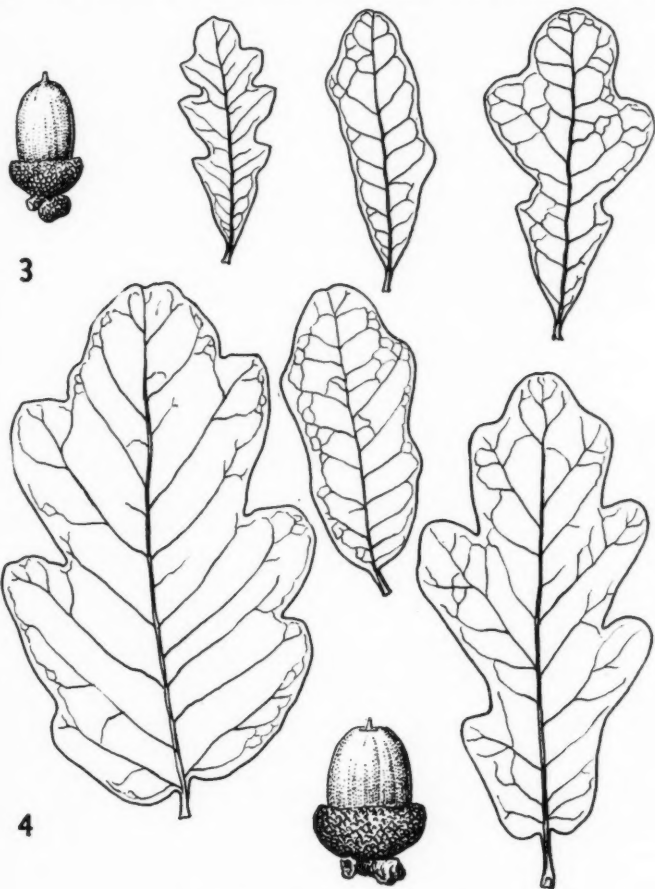


Fig. 3. *Quercus Durandii* var. *breviloba*.

Fig. 4. *Quercus Laceyi*.

species. The southeastern tree may, therefore, be known as *Quercus Durandii* var. *austrina*, comb. nov.

It may be noted that in the description of *Quercus austrina* material of *Q. Durandii* as here defined was apparently also taken into consideration, since the leaves were said to be white tomentose beneath but soon glabrous. This statement was continued in the description in the Manual of the South-eastern flora (1933), but in the key the two species are distinguished as: Leaf-blades glabrous, at least when fully grown, green beneath—*Quercus austrina*; leaf-blades persistently pubescent and white beneath—*Quercus Durandii*.

Walter in his Flora Caroliniana, page 235 (1788) published the name *Quercus sinuata* with a brief Latin description. And Ashe⁷ suggested that this was an earlier name for *Quercus austrina*, calling attention to the fact that the tree is found not far from Walter's region. But it is evident that he had some of the characters of *Quercus Durandii* in mind and not those of the more eastern tree. And later after becoming better acquainted with *Q. austrina* he in effect admitted that he had been mistaken⁸ since the acorn-cups of that tree are not shallow, the character mentioned in Walter's description on which he had mainly relied. *Quercus Durandii* is not known in Walter's region and the tree could scarcely have been known to him. But there are other reasons for rejecting the idea that he was describing any form of that species. The description is so short that it is worth while to quote it:

(*Quercus*) *sinuata* 12. foliis sinuatis laevibus obtusis, supra pallidis subtus subglaucis, glandibus mediocribus globosis calyce subplano.

The leaves of both varieties of *Quercus Durandii* are bright green and glossy and never pale above; the acorns are small, ovoid or oblong-cylindric and not globose or subglobose. In no character except possibly in the shape of the leaves can this description be reconciled with *Q. austrina*.

Engelmann⁹ believed that *Quercus sinuata* was a hybrid between *Q. laevis* and *Q. nigra*, which seems to be a more reasonable interpretation. But in my opinion, the description seems rather to indicate a hybrid between *Q. cinerea* and some other species, as that tree also grows in the coastal region of the Carolinas and is known to hybridize with several other oaks. But until a specimen named *Quercus sinuata* by Walter can be seen, the name must remain a doubtful one, and it is treated here as a *nomina dubia*.

Another oak that has sometimes been confused with *Quercus Durandii*, or with *Q. sinuata* where that name has been taken up for it, is *Quercus Laceyi* Small,¹⁰ which is found rather locally in the canyons of the south-western part of the Edwards Plateau of Texas. Although the range is limited, this species is not rare in some localities, and I have seen specimens from Kendall, Kerr, Bandera, Kimble, Real, Menard, Edwards and Uvalde counties. Trelease¹¹ considered it a form of *Q. breviloba*, stating: "What would

7 Proc. Soc. Amer. Foresters, 11:89. 1916.

8 Bull. Charleston Mus. 14:11. 1918.

9 Trans. Acad. Sci. St. Louis, 3:400. 1877.

10 Flora S. E. U. S., 353. 1903.

11 Mem. Nat. Acad. Sci. 20:102. 1925.

be taken for *Q. breviloba*, except that its cup scales are more thickened, is *f. Laceyi* (*Q. Laceyi* Small).” However, it is well distinguished from *Quercus Durandii* or any of its varieties and it is doubtful whether they are its closest allies. The reason for including it here is that it is a little known species and has been seen by few botanists or collectors.

Quercus Laceyi is a small tree up to 10-12 m. tall with thick, pale, deeply fissured bark. The leaves are mostly oblong or oblong-obovate in outline, 2-20 cm. long, 1-7 cm. wide, runcinate or with 1-3 pairs of low, rounded lateral lobes, rounded or emarginate at the apex, rounded to subcordate or very rarely narrowed at the base, pubescent beneath when young, at maturity thin but firm, glabrous, blue-green above, slightly paler and reticulate beneath; fruit sessile or short peduncled; nut short-cylindric, 1.5-2.3 cm. long, .8-1.5 cm. thick, rounded or flattened at the base, enclosing about 1/3 of well-developed nuts, covered with pale pubescent scales with conspicuously corky thickened bases.

The thick ridgy bark as well as the characters of the leaves and fruit separate *Quercus Laceyi* from *Q. Durandii* and its varieties, and it is conspicuous and easily distinguishable in the field at long distances on account of the blue-green or “smoky” color of the foliage. Collections from Kendall County, Texas, where this species is rare and where *Quercus Durandii* var. *breviloba* is abundant show intermediate characters and suggest hybridization.

The accompanying key and figures may help in distinguishing the different species and varieties. I am under obligation to Mr. Gordon Dillon for preparing the figures.

1. Leaves cuneate at base, dark or yellowish green and glossy above, not conspicuously reticulate beneath at maturity; cups of acorns thin-edged, the scales not thickened or only slightly thickened at base. Trees or shrubs with scaly bark.3
2. Leaves entire or variously and often asymmetrically lobed, pale and silvery or green beneath; cups of acorns enclosing 1/4 or less of well developed nuts.2
3. Mature leaves thin; cup of acorn very small and often disc-like, enclosing 1/5 or less of well developed nuts, the scales thin and never corky thickened at base. A tree usually in alluvial soil of coastal plain.1. *Q. Durandii*
3. Mature leaves firm to subcoriaceous; cups of acorns rounded and enclosing about 1/4 of well developed nuts, the scales sometimes slightly thickened at base. A shrub on limestone hills, or rarely a small tree in protected places.1-a. *Q. Durandii* var. *breviloba*
2. Leaves normally all lobed at least toward apex, usually symmetric, green beneath; cups of acorns rounded or turbinate enclosing about 1/3 of well developed nuts. A tree along streams or on low hills of the southeastern coastal plain.1-b. *Q. Durandii* var. *austrina*
1. Leaves rounded, truncate or subcordate at base, conspicuously blue-green above and reticulate beneath at maturity; cups of acorns thick, the scales much thickened at base. A tree with thick ridgy bark, along streams or in canyons of the Edwards Plateau, Texas.2. *Q. Laceyi*

ARNOLD ARBORETUM,
JAMAICA PLAINS, MASSACHUSETTS.

Plant Succession on Abandoned Farm Land in the Vicinity of New Orleans, Louisiana

Juanda Bonck and W. T. Penfound

Introduction

In the latter part of the Nineteenth Century the area in the immediate vicinity of New Orleans was planted largely to sugar cane. In 1912 considerable decline in yield was observed as a result of the sugar cane mosaic. By 1926 the sugar production had fallen from 300,000 to 47,000 tons. Not one of the large plantations survived this blow in the area under consideration and at the present time these plantations are divided into small truck farms or have been largely abandoned.

The purpose of the present investigation was to determine the plant succession on all types of these abandoned fields in the vicinity of New Orleans. After a few reconnaissance trips we decided to limit our studies to the better drained lands on the natural levees of the Mississippi River. Furthermore we decided to eliminate all fields in drainage projects and those which had been subjected to fire, mowing, or grazing. The investigation was carried out from October, 1940 to February, 1942.

The area considered is located along both banks of the Mississippi River within a distance of ten miles from New Orleans. The levee gradually slopes away from the river to the swamps, from one-half to two miles away. The higher portions of the levee consists principally of Yazoo sandy loam, whereas the land nearer the swamps is either clay loam or muck. In order to avoid a great variation in soil texture, all plots chosen for study were located not more than one-half mile from the river.

The climate of New Orleans is sufficiently mild to permit the growth of plants throughout the entire year. The coldest months are January and February, which have mean monthly temperatures of 54.3° F. and 56.8° F., respectively. The rainfall is ample for excellent growth of plants throughout all periods of the year because of its relatively even distribution and total quantity (59.58 inches annually). The mean annual temperatures during the period of our study (1940-1942) closely approximated normal. No freezing temperatures were experienced during 1941. Although the temperatures during January, 1942, dropped below the freezing point for four days, no unusual damage to vegetation was experienced. The rainfall for 1940 was 20 inches above the yearly normal, but the precipitation for 1941 and early 1942 closely approximated the long-term average.

Methods

In the course of several reconnaissance trips we attempted to locate undisturbed fields which had been abandoned from one month to as long as twenty-five years. The dating of the plots was determined primarily by questioning the occupants of the property and by counting the growth rings in the largest woody plants. Of the 87 fields chosen for study 56 were eliminated from the final record because of burning, grazing or cutting. Furthermore, a few other fields were abandoned because of the decision of the farmer to clear and plow the land under investigation. This was especially true in the winter of 1941-1942 when an increased demand for vegetables caused a considerable increase in cultivation in the New Orleans hinterland.

In practice monthly visits were made to each plot and all plants were collected and identified with the aid of Small's Manual of the Southeastern Flora (1933). The sampling methods utilized were those outlined by Braun-Blanquet (1932). Quadrats two decimeters square were utilized in studying the earlier stages on abandoned fields. Quadrats one meter square were employed in analyzing most herbaceous vegetation, whereas quadrats five meters to a side were used in sampling shrub communities. Although data on frequency were taken, these data are not considered of sufficient value for inclusion in the tables.

Results

Early in our study we found that the time of plowing determined the type of annual weedy vegetation that was to appear on the abandoned fields. Fields plowed in the late fall (Oct., Nov. and Dec.) were populated with a weed stage in which *Lamium amplexicaule* and *Alsine media* were predominant (table 2, fig. 1). *Lamium* was predominant on the ridges, whereas *Alsine* was relatively more abundant in the furrows of the abandoned cane lands. Both *Lamium* and *Alsine* became established by early December and were still present in April. Many other so-called "winter annuals" ecize in January or February and disappear at about the same time as *Lamium* and *Alsine*. Among these species, *Carara didyma*, *Gnaphalium purpureum*, and *Veronica peregrina* were abundant on the ridges, whereas *Echinochloa colona* and *Cyperus rotundus* were numerous in the furrows. By the first of April a leguminous weed stage was established, consisting of such spreading species as *Melilotus indica*, *Medicago hispida*, *Medicago lupulina*, and *Medicago arabica*.

In vacant lots in New Orleans such species as *Poa annua*, *Hordeum pusillum*, *Erigeron philadelphicus*, etc. are abundant. Such plants, however, are rarely found in the weed stages on abandoned farm land. Since young abandoned fields appear to be an excellent area for invasion by such species, it is difficult to account for their scarcity in such fields. Observations on vacant lots and roadsides reveal an abundance of such grasses as *Paspalum dilatatum*, *P. urvillei*, and *Sporobolus poiretii*. Since these species are also abundant in pastures, it is evident that they thrive under conditions of cutting and grazing. It is possible that cutting or grazing may be necessary for their continuance, since they occur rarely on abandoned farm lands in the area.

With the gradual dying out of *Melilotus* and species of *Medicago* in May comes a gradual increase in such summer grasses as *Syntherisma sanguinale*,

and *Capriola dactylon* (table 3, fig. 2). Other important species, at least locally, include *Eleusine indica*, *Echinochloa colona*, and *Leptochloa filiformis*. The thick cover of these summer grasses remains on the land throughout the autumn.

As heretofore stated, the annual weedy vegetation of recently abandoned fields is closely related to the time of plowing. Plots plowed in the fall exhibit three annual weed stages: the winter weed stage, the leguminous stage, and the summer grass stage (table 1). Plots plowed in winter (Jan., Feb., Mar.)

TABLE 1.—Successional march of communities on abandoned agricultural lands in the vicinity of New Orleans, Louisiana.

Year	Months	Community
1st	Dec. - Mar.	Laminum - Alsine
1st	Mar. - May	Melilotus - Medicago
1st	May - Dec.	Syntherisma - Capriola
2nd	Jan. - May	Syntherisma - Capriola
2nd	June - Nov.	Solidago hirsutissima
3rd - 7th	Jan. - Dec.	Solidago hirsutissima
7th - 10th	Jan. - Dec.	Solidago - Cerrothamnus
10th - 25th	Jan. - Dec.	Cerrothamnus ceriferus
25th - 50th	Jan. - Dec.	Cerrothamnus - Quercus
50th - 200th	Jan. - Dec.	Quercus virginiana?

TABLE 2.—The annual weedy vegetation of fields plowed in October, November, or December includes a considerable number of species. (Based on 11 records of 5 plots.)

Species	Month						
	N	D	J	F	M	A	M
<i>Lamium amplexicaule</i>	x	x	x	x	x	x	
<i>Geranium carolinianum</i>	x	x	x	x	x	x	x
<i>Alsine media</i>		x	x	x	x	x	
<i>Carara didyma</i>		x	x	x			
<i>Cardamine pennsylvanica</i>		x	x	x	x	x	
<i>Cerastium viscosum</i>		x		x	x	x	x
<i>Sonchus asper</i>		x	x	x	x	x	x
<i>Xanthoxalis Brittoniae</i>			x	x	x	x	
<i>Ranunculus muricatus</i>			x	x	x	x	
<i>Poa annua</i>			x	x	x	x	
<i>Trifolium repens</i>			x	x	x	x	x
<i>Verbena bonariensis</i> (seedlings)			x		x	x	x
<i>Ambrosia aptera</i> (seedlings)				x	x	x	
<i>Veronica peregrina</i>				x	x	x	x
<i>Veronica agrestis</i>				x	x		
<i>Callitriche palustris</i>				x			
<i>Gnaphalium purpureum</i>				x			x
<i>Rumex crispus</i>				x		x	x
<i>Medicago hispida</i>				x		x	x
<i>Medicago lupulina</i>					x	x	x
<i>Medicago arabica</i>				x		x	x
<i>Melilotus indica</i>						x	x
<i>Holcus halepensis</i>					x	x	x
<i>Hordeum pusillum</i>				x	x	x	x
<i>Samolus floribundus</i>					x		
<i>Raimannia laciniata</i>					x	x	x
<i>Specularia biflora</i>					x	x	x
<i>Specularia perfoliata</i>						x	x
<i>Erigeron philadelphicus</i>						x	

<i>Plantago Rugelii</i>	x	
<i>Phalaris angustifolia</i>	x	
<i>Lepidium virginicum</i>	x	
<i>Stachys agraria</i>	x	
<i>Cyclospermum ammi</i>	x	
<i>Capriola dactylon</i>	x	x
<i>Cyperus rotundus</i>	x	x
<i>Ranunculus pusillus</i>	x	
<i>Vicia ludoviciana</i>	x	
<i>Dracopis amplexicaulis</i>		x
<i>Gymnostyles anthemifolia</i>		x
<i>Solidago hirsutissima</i> (seedlings)		x

TABLE 3.—By the end of the first growing season *Syntherisma sanguinale* and *Capriola dactylon* are the predominant species as indicated by their high cover percentages.

Species	App. cover (Percent)
<i>Syntherisma sanguinale</i>	30
<i>Capriola dactylon</i>	10
<i>Eleusine indica</i>	4
<i>Echinochloa colona</i>	2
<i>Achyranthes philoxeroides</i>	1
<i>Leptochloa filiformis</i>	<1
<i>Rumex crispus</i>	<1
<i>Diodia virginiana</i>	<1
<i>Commelina longicaulis</i>	<1
<i>Solidago hirsutissima</i>	<1
<i>Chamaesyce hyssopifolia</i>	<1
<i>Aster exilis</i>	<1
<i>Cyperus rotundus</i>	<1
<i>Verbena bonariensis</i>	<1
<i>Physalis angulata</i>	<1

TABLE 4.—*Solidago hirsutissima* is the major dominant of the goldenrod community.

Species	App. cover (Percent)
<i>Solidago hirsutissima</i>	35
<i>Andropogon glomeratus</i>	4
<i>Verbena bonariensis</i>	4
<i>Ambrosia aptera</i>	1
<i>Paspalum urvillei</i>	<1
<i>Andropogon virginicus</i>	<1
<i>Aster sp.</i>	<1
<i>Iva ciliata</i>	<1
<i>Aster exilis</i>	<1
<i>Capriola dactylon</i>	<1
<i>Cyperus rotundus</i>	<1
<i>Medicago hispida</i>	<1
<i>Medicago lupulina</i>	<1
<i>Vicia ludoviciana</i>	<1
<i>Hordeum pusillum</i>	<1
<i>Geranium carolinianum</i>	<1
<i>Melilotus indica</i>	<1
<i>Erigeron philadelphicus</i>	<1
<i>Rubus spp.</i>	<1
<i>Cerastium viscosum</i>	<1
<i>Trifolium repens</i>	<1

TABLE 5.—A comparison of the relative importance of species in the shrub (*Cerothamnus ceriferus*) community in the thirteenth and twenty-fifth year after the fields were abandoned.

Species	Shrub stratum	App. Cover, per cent	
		13th	25th
<i>Cerothamnus ceriferus</i>		50	65
<i>Svida asperifolia</i>		5	1
<i>Sambucus canadensis</i>		<1	2
<i>Quercus virginiana</i>	<1
Transgressive species			
<i>Rubus</i> spp.		8	3
<i>Sambucus canadensis</i>		<1	6
<i>Ampelopsis arborea</i>		<1	<1
<i>Toxicodendron toxicodendron</i>		<1	<1
<i>Viola langloisii</i>	2
<i>Galium aparine</i>	1
<i>Urtica chamaedryoides</i>	<1
<i>Sanicula canadensis</i>	<1

lack the winter weed stage and those plowed in the spring (Apr., May, June) lack both the winter weed and the leguminous weed stages. By the middle of the first summer after abandonment all fields (regardless of the time of plowing) resemble one another very closely in the thick cover of grasses which remains on the land throughout the winter.

The transition from the annual weed stage to the perennial stage is accomplished during the second growing season (tables 1 and 4). In February of this period dead grasses of the previous summer still maintain a heavy cover of the soil but abundant young plants of *Solidago hirsutissima* are to be found under the grass cover (Figs. 1 and 2). By June of the second growing season the perennial weed stage is fully established. *Solidago* is the only important dominant in this community, although *Andropogon glomeratus* and *Verbena bonariensis*, because of their conspicuous inflorescences, give the appearance of predominance (table 4). Because of its great cover, it is probable that the total mass of plant material formed by *Solidago hirsutissima* is greater than that of all the other components in this community.

The goldenrod community persists for seven years but is gradually replaced by the tenth year by the shrub community. A considerable seasonal change occurs in the goldenrod community, especially during the early spring, at which time such annuals as *Melilotus*, *Medicago* spp., etc. are present in considerable numbers. This group includes all the species listed below *Cyperus rotundus* in table 4.

The transformation of the goldenrod community into the shrub community is a very gradual one. Some shrubs may become established during the second year after abandonment. The number and size of the shrubs gradually increase with the years until final establishment of the shrub community is accomplished by the tenth year (Fig. 3). Between the seventh and the tenth years *Solidago* becomes increasingly shaded out, as is true of the other predominant species in the goldenrod community. By the tenth year the shrub



Fig. 1. The annual weed stage (*Lamium-Alsine*) is already present by December, on land that is plowed in October. Perennial weed stage at the right.

Fig. 2. The summer grass stage (*Syntherisma-Capriola*) is fully established by the end of the first growing season.

cover is much greater than that of the herbaceous cover and by the thirteenth year all of the predominant species of the goldenrod community have been eliminated.

The wax myrtle, *Cerothamnus ceriferus*, is the dominant species in the shrub community (table 5, fig. 3). Locally the dogwood, *Svida asperifolia*, may be predominant. The same is true of the buckbrush, *Baccharis halimifolia*, and the elderberry, *Sambucus canadensis*, especially on relatively moist sites. In the thirteen-year-old stand investigated the wax myrtle presented a cover of approximately 50 per cent, with an average height of 14 feet and an average diameter of 2.6 inches. Twined among the branches of the wax myrtle were numerous vines, especially the pepper vine, *Ampelopsis arborea*, and the poison ivy, *Toxicodendron toxicodendron*.

The 25-year-old stand had the appearance of a young forest, with a closed crown which allowed the penetration of relatively little light (Fig. 4). The wax myrtle had increased its cover to about 65 per cent. The average height had increased to 24.3 feet and the average diameter had increased to 4.3 inches. In this stand the dogwood was absent but in its stead were numerous specimens of the persimmon, *Diospyros virginiana*. The scant, herbaceous cover consisted of true forest herbs, including species of *Galium*, *Viola*, *Urtica*, and *Sanicula* (table 5). Of considerable interest was the discovery of numerous small live oaks, *Quercus virginiana*, (table 5). These seedlings averaged two feet in height and about 160 per acre. The evidence suggests that the shrub



Fig. 3. The dominant species, *Solidago hirsutissima*, of the perennial weed stage still exhibits high coverage in the seventh year, despite invasion by *Cerothamnus ceriferus*, of the shrub community.

community may give way to an evergreen oak forest in which the live oak is a predominant. This assumption is given support by the presence of evergreen oak forests along Metairie and Gentilly ridges on the outskirts of New Orleans, along the Mississippi River ridge and on nearly every uncultivated cheniere in southeastern Louisiana.

Discussion

In the southeastern states relatively few studies have been made of the successional stages on abandoned farmlands. Wells (1928) described a succession with a pioneer stage of *Syntherisma*, a middle stage of *Aster*, *Daucus*, *Eupatorium*, and *Solidago* and a final stage of species of *Andropogon*. Billings (1938) listed *Syntherisma* as an important pioneer and *Andropogon* as a predominant in the perennial weed stage. McQuilkin (1940) found that "dominance in old-field vegetation typically passes from annual weeds, to perennial weeds, to *Andropogon*. . . ." Oosting (1942) found much the same sequence with fields abandoned for one year being dominated by *Leptilon* and *Syntherisma*, two-year fields by *Asters* and *Ambrosia*, and three-year fields by *Andropogon*. All of these investigations showed that the succession passed from an annual weed stage (usually including *Syntherisma*) to a perennial weed stage (often including *Solidago*) and ending (the herbaceous phase) with *Andropogon*. In our area *Andropogon glomeratus* was present by the second year but never became a predominant species in the perennial weed



Fig. 4. The shrub community in the 25-year old field approximates a true forest aspect.

stage, presumably due to the competitive ability of *Solidago hirsutissima*. In our area, therefore, the genus *Andropogon* never becomes a predominant plant in any of the successional stages.

In the New Orleans area, Howard and Penfound (1942) investigated the early succession on the alluvial dunes deposited by floodwaters of the Mississippi River in the Bonnet Carré floodway in the winter of 1937. They found one community dominated by *Panicum capillare* and a variant of the same in wetter sites in which *Panicum dichotomiflorum* and *Cyperus esculentus* were the predominant plants. Neither of these communities were encountered on abandoned fields. In fact only one-third of the species present on the floodway dunes were encountered in the field subser. In a study of the plant succession on a roadbed about thirty miles west of New Orleans by the junior author, 70 percent of the species were common to the successional stages on abandoned fields. Although certain of the early species were different, a similar series of stages from annual to perennial weed stages occurred. Furthermore, there was a gradual increase over a four-year period in the relative abundance of *Solidago hirsutissima*. The degree of correlation between the species list on the roadbed and that of abandoned fields is surprising in view of the fact that this roadway was cut through a former cypress swamp, and since the soil was much heavier than that of the field subser investigated.

Summary

1. Plant succession on abandoned agricultural land along the Mississippi River in the vicinity of New Orleans proceeds through the following broad stages: annual weed stage, perennial weed stage, and shrub stage.

2. Plots plowed in the autumn (October, November and December) have such annuals as *Lamium amplexicaule* and *Alsine media* as the important pioneers; by April, *Melilotus indica* and species of *Medicago*; and by June, summer grasses such as *Syntherisma sanguinale* and *Capriola dactylon*.

3. Plots plowed in the winter (January, February and March) have *Melilotus* and species of *Medicago* as pioneers, whereas plots plowed in the spring (April, May and June) have summer grasses such as *Syntherisma* and *Capriola* as the earliest invaders.

4. By the end of the first summer following abandonment, fields of each group (regardless of time of plowing) closely resemble one another in the cover of summer grasses.

5. The initiation of the perennial weed stage occurs during the second growing season after cultivation. By the second summer, *Solidago hirsutissima* is the predominant species.

6. From the second year onward shrubs increase in size and density until about the tenth year when the shrub stage is established.

7. A field abandoned for 25 years has the appearance of a young forest

with tall wax myrtle shrubs forming a dense canopy, and with a relatively sparse herbaceous layer.

8. The final stage of plant succession in this locality is not known, although it is probable that *Quercus virginiana* is an important component.

9. Certain genera such as *Syntherisma*, *Solidago*, and *Andropogon*, which are important constituents of successional plant communities in the southeastern states generally, are also prominent species on abandoned farmland in the New Orleans area.

ACKNOWLEDGMENTS

The authors wish to express their appreciation to Mr. Thomas F. Hall, Mrs. Faith P. Mackenness and Mr. R. T. Perkins for assistance in the field work and especially to Mr. Cedric Sidney for help in connection with the field study of the shrub community.

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LOYOLA UNIVERSITY,
AND
TULANE UNIVERSITY,
NEW ORLEANS, LOUISIANA

Book Reviews

CONSERVATION OF RENEWABLE NATURAL RESOURCES: SOME FUNDAMENTAL ASPECTS OF THE PROBLEM. By Raphael Zon, William S. Cooper, Gustaf A. Pearson, Homer L. Shantz, A. E. Douglass, Charles G. Abbot, Paul B. Sears, Ellsworth Huntington, Morris L. Cooke, Samuel T. Dana, Milton S. Eisenhower, Julian F. McGowin. University of Pennsylvania Press, Philadelphia, Pa. 1941. vi + 200. \$2.50.

In the short space of two hundred pages twelve authorities in various phases of conservation of natural resources have given a clear picture of the events which have led to many national problems and the future responsibilities of citizens and administrators in total conservation. The volume should be used as required reading for every college student and should also be read by every serious citizen.

The subject matter of this volume is divided into these three major headings, (1) the natural vegetation of the United States as a guide to current agricultural and forestry practice, (2) climatic cycles in relation to the theory and practice of conservation, and (3) the administrative task of conservation—private and public. Each of these headings is further subdivided.

Natural vegetation as a key to conservation practices by Raphael Zon emphasizes that "natural vegetation is the integrated expression of environment—climate, soil, and animal life. From a physical standpoint it should, therefore, be a good criterion of the potentialities of land for different uses." Economic considerations have in the past had much to do with the development of land. The early method of trial and error in land utilization is now being replaced. "With the contraction of agriculture, due to loss of many of our foreign markets and to higher production obtainable from smaller areas, and with the growing need for finding uses of land other than agriculture, a more clearly rounded-out, better planned land use is coming into existence to replace the earlier planless exploitation of the land. In this new era, plant science can make and is making a valuable contribution. . . . not only in determining the adaptability of land for agriculture but also in indicating means of perpetuating our forests, reforesting waste land, providing the proper habitat for our wildlife, controlling surface run-off, and preventing excessive soil erosion."

The thesis for "Man's Use and Abuse of Native Vegetation: The Lessons of the Past and the Prospects for the Future" by William S. Cooper is "that man school himself to realize that after all he is but a single species of animal, albeit an important one, involved with all other organisms, both plants and animals, in a complex web of community relations, where man is far more dependent upon his fellows than they are upon him." When the white man came to North America the native vegetation in general consisted of forest, grassland and desert. Man worked his way from the Atlantic to the Pacific by hit-or-miss, trial-and-error methods of exploiting the natural resources. The result was the destruction of the pine forests of the northeast, the mutilation of the forests of the southeast, the great reduction of the deciduous forest, the near extinction of the tall-grass prairies and modification and destruction of the remaining types. Although this 'muddling' across the continent was accompanied by the development of agriculture in the wheat, corn, cotton and citrus belts, many very serious problems were produced which only now are realized.

Many of the mistakes made by the trial-and-error utilization of the native vegetation can be rectified but this means that "man needs to know the vegetation with which he has to deal in all its phases and from all viewpoints. His knowledge must be free from assumption and guesswork as far as is humanly possible; its various elements must be coordinated in mutual support." In order to attain such information man should know the life histories of key species, the nature and development of communities, the dis-

tribution of communities over the continent and a knowledge of the environment as a background for all of these considerations.

As a nation we are now faced with the serious problems of the "(1) proper treatment of such vegetation as still retains to a considerable degree its original constitution, so that it may give maximum value without deterioration; (2) rehabilitation of vegetation that has been so abused that it now stands apparently useless, with discovery and development of new uses for it." Federal, state and private endeavors have started many worthwhile projects of preserving, protecting and rehabilitating natural vegetation. Dr. Cooper concludes that man "realizes that in his own interest he must allow to his fellow citizens of the organic world, in particular the plants of all sorts which he utilizes, the greatest possible freedom to develop in their own individual ways and to carry out their special community roles; in other words, that governmental paternalism must be reduced to a minimum. He realizes, finally, that such a policy, involving a delicate balance between freedom and control, requires abundant and accurate knowledge, which derives from one source alone—fundamental research."

How native vegetation may be used as a guide for land use is the subject of "What Forest Trees Tell About Climate and Soil" by Gustaf A. Pearson. This is exemplified in the vegetation of the southwestern United States where seven broad zones of vegetation and climate are recognized. The characteristic and conspicuous desert trees of paloverdes, ironwood, mesquite and giant cactus, always indicate mild winters. With irrigation bountiful crops flourish in both summer and winter. The desert grassland (although lacking trees except in transition zones) is extensively used for grazing livestock. The woodlands have rainfall inadequate for successful farming unless irrigation is used. The ponderosa pine, or western yellow pine indicates areas of higher precipitation than the preceding types. Timber is the major crop of this area. Above the ponderosa pines is a forest composed of Douglas fir, white fir and limber pine. Their highest value (even above commercial value) is for the preservation of watersheds and for recreation. The spruce forests cover the high mountain slopes and indicate the coldest and wettest climate of the forest types. Above timber line grasses, sedges and rushes provide pasture during the short summer. An interpretation of the conditions which accompany native vegetation can result in using plants as indicators for land utilization. Dedication of the land to its highest use "calls for the cooperative effort of biologists of all classes, of geologists, soil specialists, engineers, economists, sociologists, and legislators; and lastly it calls for understanding and approval by the general public."

In "The Original Grassland and Desert Shrub Vegetation of the United States as a Guide to Present Day Agricultural Practice" by Homer L. Shantz, land is divided into wild land—that which is in a more or less natural condition—and cultivated land—where the vegetation is destroyed and the top soil disturbed. "Wild land always has been and will continue to be important to man. Of the world area, fully half of the land has a climate unsatisfactory for the production of cultivated crops; and only a small percentage of this semidesert land can be used with irrigation. In the United States a little more than half of the area has a favorable climate. Of the half which lies under a suitable climate, much of it is unsuitable for crop production because of unfavorable soil or topography. It seems probable that on a world basis wild lands will always exceed cultivated lands." Originally about 48 per cent of the United States was covered by forest, 38 per cent by grassland and 14 per cent by desert. Different government planning agencies have estimated that one third of the country should be kept as forest and woodlands in order to produce the necessary forest products, for watershed protection and stabilization of stream flow, for recreational purposes and for a home for wild animals and domestic livestock.

"The objective in wild land management is to allow nature to develop as rich a soil, as rich and varied a plant cover, and as varied and rich an animal population as the basic rock material and the climate and weather conditions will support." This necessitates a great knowledge of soils, climate, physiography, botany, zoology, sociology and economics. At this point Dr. Shantz divides the original grassland and desert shrub vegetation into their major communities then gives the major agricultural use of each

community. This list is made even more useful by the addition of the scientific names of the plants mentioned and a list of the references used. Three maps indicate, (1) the types of native vegetation in the United States, (2) the land which is in harvested crops, and (3) the agricultural regions of the United States.

"Dendrochronology and Studies in Cyclics" by A. E. Douglass, reviews the development of the study of correlation of tree ring studies and climate. From analyses of tree rings climatic data for 1900 years were obtained in Arizona and New Mexico and 3250 years for California. The responses of tree growth to changes in the climate are recorded in the annual increment of the stems. Thus periods of drought result in narrow annual rings while moist periods are responsible for wider rings. These ring patterns in trees prevail over large areas and make possible the correlation of ring patterns in different trees thereby allowing a method of cross dating for the establishment of a bio-climatic chronology.

Repetitions of narrow rings and wide rings at definite intervals established the study of "Cyclics" which was useful in interpreting the rhythm of climatic changes.

The following results make prognostication possible: "(1) There has been found evidence of orderly change in long periods, for example 275 years. This and other changes may depend perhaps on long slow changes in the sun; (2) from the presence of solar rotation in the recurrence of storms and from other facts we can count on solar effects in climate; the importance of such studies is obvious."

"Periodicities in Solar Variation Reflected in Weather" by Charles G. Abbot follows. For more than twenty years the Smithsonian Institution has made daily observations of the intensity of solar radiations. "The temperature and rainfall of the earth are maintained by the sun's radiation. If the sun were invariable the climates of the earth would probably be invariable too. But the sun's radiation fluctuates through a range never exceeding three per cent. These fluctuations are the main cause of weather changes."

An analysis of the twenty years of daily observation has revealed that there are ten regular periodicities of solar variation whose duration are approximately 8, $9\frac{3}{4}$, $11\frac{1}{4}$, 21, $25\frac{1}{3}$, $39\frac{1}{2}$, $45\frac{1}{4}$, 68, 91, 137 and 273 months. Although moderate success has been achieved in long range forecasting from the use of a 23 year period two obstacles have been encountered. "First, the uncertainty whether periodicities in the sun's variation continued indefinitely in the same phase, and second, the probability that even if they do, the complexity of the earth and its atmosphere might cause reversals of phase in the weather effects. . . . These investigations lead to the conclusion that the periodicities found in solar variation have continued without change of phase for at least a century. This conclusion warrants the hope that forecasts of weather, synthesized from these periods, with proper attention to the cause of phase changes explained above, may be fairly satisfactory."

In "Conservation and Changing Environment" Paul B. Sears states that the need for conservation arises whenever an unfavorable balance develops with respect to any one of these major classes of resources, (a) the changing requirements of a given community, (b) depletion or disturbance wrought by a given culture, or (c) 'natural' changes not caused by man.

Whatever the change in environment the human community must adjust to the change. This adjustment involves careful planning with the aggressive support and participation by local communities in order that conservation may be effected.

"Climatic Pulsations and an Ozone Hypothesis of Libraries and History" by Ellsworth Huntington proposes a new hypothesis which has many interesting psychological and sociological implications. "According to the ozone hypothesis, variations in solar activity give rise to variations in storminess, and hence in the degree to which waves of ozone sweep outward from polar regions, or are produced in the rain and winds of storms. Hence, during periods of maximum solar activity the stimulating quality of the weather tends to increase. This increase presumably takes place all over the world, but is at a maximum, and perhaps at too high a level, in relatively high latitudes. The value of the ozone hypothesis from this standpoint lies in the fact that it provides a more concrete and definite basis for the psychological stimulus than has hitherto been

available. . . . How great these effects have been we cannot yet tell, but we can at least suggest that they have played some part in history. Farther than this we cannot yet go, but each step in our study of man's relationship to weather makes it more clear that climatic pulsations exert wide and diverse effects upon human welfare."

"On Total Conservation" by Morris L. Cooke, emphasizes the necessity of planning the completed job in order to work intelligently and efficiently in the multiple problems in conservation. The United States is not a permanent country because the natural cover has been destroyed in the pursuit of cash crops and the top soils have been greatly removed by floods. In order to salvage that which has been disturbed and replace some of the destroyed natural resources it is necessary to have a program of total conservation embracing the support and efforts of farmers, stockmen, sportsmen, nature lovers, water and power purveyors, railroad men, and bankers. "It has been estimated that the United States has only seventy-five to one hundred years to go as a virile nation unless brave remedial measures are set up."

"In Natural Resources and the States" Samuel T. Dana states that "the first responsibility of any commonwealth is to assure its own prosperous perpetuity. An abundant and continuing supply of natural resources is essential for its material prosperity. Therefore society has not only the right but the duty to take such measures as may be necessary to prolong the supply of those resources which are exhaustible and to perpetuate the supply of those which are renewable." Public apathy, rugged individualism, and governmental ineptitude are believed to be chief difficulties in an adequate conservation program. These difficulties can be overcome by cooperation. The author is of the opinion that "conservation of natural resources is largely a problem in the fields of economics and political science. A knowledge of biology and engineering is of course essential in the handling of organic resources, but it must be utilized in ways that are economically, administratively, and socially sound." If an amount of money equivalent to a fraction of the sum which is spent to prevent our resources from falling into enemy hands were spent on conservation, the citizens of the United States would profit immeasurably for many generations to come.

"Federal Responsibilities in Total Conservation" is the subject of a chapter by Milton S. Eisenhower. An inventory of the damage in the United States shows 50 million acres ruined, three-fourths of the topsoil gone from 225 million acres; and one-fourth to three-fourths gone from 775 million acres. Such a volume of destruction demands a concerted effort to achieve total conservation using the appropriate physical measure with full cognizance of the changing economic and social factors. The development of a conservation policy has been slow because of the widespread lack of recognition of the total destruction of resources in addition to the pressure of economic conditions upon individual owners of resources causing them to ignore the need of conservation. These difficulties were augmented by the first World War, the consequent disruption of world trade, and the industrial depression. The following things necessitated government assistance: national adjustment was needed, the suddenness of the need for change, the disappearance of frontiers, lack of an alternative system of production to shift to, and the disappearance of opportunities in the cities caused by the industrial depression. These problems caused Congress to attempt legislation for agricultural adjustment, surplus disposal, marketing agreements, erosion control, flood control, farm forestry, water facilities, rehabilitation and tenancy for the purpose of maximum benefits and permanent maintenance of resources.

The participation of private land users in total conservation is essential. Government interest and public response are needed to back the actual participants of any conservation program. The integration of these forces is necessary and fortunately much is now being undertaken in this line. For the first time in this country, waste is being deplored with a realization of how it may be combated.

Julian F. McGowin concludes this volume with a chapter entitled "The Forest Problems Can Be Solved by Increased Production and Use." He believes that the human element is an obstacle to progress in forestry. Habits and customs of many rural areas must first be overcome before fire protections and forest management can be effective. When these things are accomplished increased production of forest products can follow.—D. PARKER.

ELEMENTS OF BACTERIAL CYTOLOGY. By Georges Knaysi. Comstock Publishing Company, Inc., Ithaca, New York, 1944. xii + 209 pp., 91 text figures and 10 plates. \$3.50.

More than thirty years ago Arthur Meyer published his now classic "Die Zelle der Bakterien." Meyer's work has remained through the years the principal reference volume for the cytologist interested in bacteria, and for the bacteriologist interested in cytology. But current emphasis on microorganisms in biological research has greatly increased the need for an up-to-date cytology of bacteria, and until recently the only modern comprehensive survey was that of I. M. Lewis, published in *Bacteriological Reviews* in 1941. Whereas Lewis' treatment is excellently conceived and executed, it unfortunately lacks both much needed illustrations and sufficient space for detailed exposition. For these reasons, Professor George Knaysi's amply illustrated "Elements of Bacterial Cytology," dedicated to giving "a clear conception of the bacterial cell according to what is judged to be the best of present knowledge," may be expected to prove of considerable interest to bacteriologists, cytologists and geneticists alike.

The text comprises an introductory chapter which cursorily deals with methods of observing bacteria, six chapters devoted principally to morphological problems of the bacterium, single chapters on physical and chemical properties of bacterial membranes, bacterial division, staining and bacteria cultures, and three concluding chapters devoted to the cytology of actinomycetes, spirochetes and myxobacteria. Thereafter follows a bibliography containing nearly 300 titles, as well as five dated citations to unpublished work by Knaysi and his students. The bibliography also serves as an author index, and only three of the titles (one of which is the recent review by Lewis!) receive no mention in the text. The index is fairly complete and more than ten pages long. The 91 figures and ten plates are for the most part well chosen and reproduced, although in certain cases they do not show clearly what they are intended to illustrate (e.g., Fig. 30 does not convincingly show deposition of new crosswalls at *b* as stated in the legend, and the flagellation of the sporangium in Fig. 37 is indeed very difficult to make out).

Although Knaysi asserts that special pains have been taken to make the presentation agree with present knowledge in bacteriology and the other sciences with which bacteriology is associated, the reviewer feels that the book loses much of the value it might have possessed because Knaysi either totally failed to consider the problems dealt with in the light of information from fields outside of bacteriology (e.g., nuclear cytology), or else delved outside of his field into materials of historical interest only (e.g., the literature discussed under "permeability of the cell membrane"). Certainly the introductory remarks of the first page do not logically lead to the observation that "the cell of bacteria is a real cell similar to the cell of other microorganisms." No criteria of cellularity are posed nor are any considerations entertained of the type so ably discussed by Dobell many years ago in his essay on the principles of protistology. The reader who is not a bacteriologist, therefore, must, either revise his notions of a cell or else accept the statement on faith. Furthermore the discussion of the problem of a nucleus in bacteria falls far short of what is desirable, and this very largely because Knaysi appears to be unacquainted with recent work in other relevant fields. He fails to set up explicit and adequate criteria based upon what is known about nuclei of typical cells, by which nuclei may be recognized in bacteria if they do in fact occur in these organisms. In spite of certain of his remarks, Knaysi seems to believe that if an organism has a system for inheritance (as bacteria do), it must necessarily be provided with a nucleus (or, as he sometimes terms it, "nuclear material"). After examining some of the older and more recent hypotheses and evidence (unfortunately omitting all mention of Robinow's recent and important work), the conclusion is drawn "that bacteria contain nuclear material which, depending on conditions yet unknown but probably related to environment and development, may be diffuse in the protoplasm or may be partly or totally differentiated into a nucleus." Thereafter follow statements of a cautionary nature which, had Knaysi himself abided by them, a much more satisfactory discussion might have been written. Although there have been many claims of the discovery of sexual processes in bacteria, Knaysi fails to consider them topically in spite of the fact that his belief in a bacterial nucleus is compatible with such claims.

The crux of the matter lies in recent demonstrations and reports that mutations of

genes in higher forms and "dissociation" in bacteria may be brought about by comparable dosages of X-rays as well as by those wave-lengths of ultra-violet light which are heavily absorbed by nucleoproteins. Furthermore the rate of spontaneous change in bacteria is similar to the normal rate in *Drosophila*. In conjunction with other information, it appears highly probable that bacteria contain hereditary determinants similar to genes, and like them associated with nucleic acids or nucleoproteins. But until sexual reproduction or its equivalent is discovered in the bacteria, no exact genetic analysis of the determinants of heredity can be made in these organisms, although cytological analysis might prove to delineate the probable mechanism of heredity if the history of the nucleoproteins and their associates can be followed. For this reason the division of supposedly constantly occurring bodies which take a positive Feulgen stain in certain bacteria at particular periods of their growth are of extraordinary interest. If mitosis for these bodies can be proven along with their numerical and qualitative constancy, then such bacteria probably do have true nuclei, although the demonstration that these bodies carry the hereditary determinants must also be made to complete the proof. If mitoses do occur, the latter demonstration could probably be made even if sexual reproduction does not occur in bacteria, although the obvious experiments would be difficult to carry out. At any rate the best that can be said at the moment is that there has been no clean cut evidence yet discovered which requires the conclusion that bacteria have nuclei, a nucleus here being understood to be a body comprised of chromosomes and dividing by mitosis.

Although the book covers to some degree most of the topics discussed by Meyer, the discussions often appear disjointed and frequently require a summary statement which is not often provided. The result is that no clear picture of the bacterial "cell" emerges. Errors, such as Knaysi's confusion of depth of focus and field depth are not rare, and in certain cases Knaysi argues to conclusions that the evidence given cannot support. For example, Knaysi's electron microscope pictures provide scant evidence (if any) of the physical properties of the cell wall such as ductility, rigidity and elasticity. Certainly these properties can only be ascertained by experiments on the living bacterium and it would have been far preferable on this score to have cited Wamoscher's work. Moreover the discussions are frequently very fragmentary. The brief treatment of methods of observation of bacteria omits any mention of dark-field microscopy, and the brief exposition of light and electron microscopy is wholly inadequate. It must be mentioned, however, that the discussion of the limitations of the electron microscope is well considered and constitutes the principal achievement of the introductory chapter. Lastly, documentation is not always satisfactory. To given an example, the chapter on staining should have referred the interested reader to the books by Conn and Zeiger.

All in all a wholly satisfactory modern substitute for Meyer's book does not emerge, despite such commendable aspects as the discussions and illustrations of the results of electron microscopy. Those interested in bacterial cytology will do well to keep Meyer's "Zelle" and Lewis' review paper on their bookshelves along with Knaysi's "Elements." No one of these is today complete, but from the three a fairly good working picture of the bacterial organism can be gained.—KENNETH W. COOPER, Princeton University.

THE BOOK OF NATURALISTS. William Beebe, editor. Alfred Knopf, New York, 1944. Pp. i-xiv, 1-499. \$3.50.

Some books review themselves. William Beebe has seen to it that this one shall, for his comments upon the selected writings of forty-five naturalists, and his two Introductions, largely anticipate and forestall the reviewer. The list of authors, as he says, could easily have been doubled, but to do so would sacrifice a fair presentation of their work. The selection ranges from Aristotle through Gesner, Linnaeus, Humboldt and Darwin, to Akeley, Wheeler, and such able youngsters as Carryl Haskins and Rachel Carson.

Without suffering actual condensation, a few items do exhibit magazine-digest symptoms. I think the brief lines from Linnaeus and the single paragraph from Osborn on elephants might well have been sacrificed to add a bit more of Humboldt, for instance—not because he was a better scientist but because, in such a book, he is better reading. Aside from this, however, I can pick no quarrel with the choices.

Seldom does Beebe fail to do justice to the authors in his editorial preambles, where he sharpens the reader's anticipation by a few words on style, or short biographical notes. I would mention just one lapse of judgment here—his comments on John Muir: "Yet with the years Muir's writings have seemed to me to have grown thinner. . . . As with some other very modern authors there are slightly too many words in Muir's paragraphs." One is entitled to his opinions about the thinness of Muir's writing, but the last remark is sheer flippancy, bringing to mind what the pot said to the kettle. Muir's essay, "The Water Ouzel," is Beebe's choice; it seems particularly admirable to anyone who has watched ouzels as Muir watched them.

These few adverse comments, however, have no weight in comparison with the deep pleasure the book brings. It may be read by samples, here and there, for many a comfortable evening, just as a naturalist on vacation will turn with satisfaction to random experiences in forest, mountain or sea.

Among the less familiar writings, none seemed to the reviewer more delightful than G. Murray Levick's "Penguins." For richness of language and beauty of imagery (without overwriting), John Farrer's "Chagola" would be hard to equal. One is glad to find something of Carl Akeley, of Wheeler, Hudson, Roosevelt, T. H. and Julian Huxley, Wallace, Darwin and Thoreau. But beyond even these the book is surprisingly versatile in styles and subjects. It is a job well done. It will be read widely, and enthusiastically recommended.—T. H. EATON, JR., University of Buffalo.

SNOWSHOE COUNTRY. By Florence Lee Jaques with illustrations by Francis Lee Jaques. The University of Minnesota Press, Minneapolis, 1944. 110 pp. 46 black and white drawings. \$3.00.

Along the north shore of Lake Superior and north to the Canadian border there is a region different from most of the United States. It is a region where severe glacial erosion has stripped much of the soil from the hills whose cores consist of ancient igneous rock. Here and there the soils have been deposited as ridges and hummocks in the form of moraines. Lakes are exceedingly plentiful since glacial scour and deposition both contribute to their origin. Some of the lakes are in rock basins and are often enclosed by steep rocky cliffs while others are in morainic depressions bordered by great spruce bogs and muskegs. The terrain is rocky and rugged. The winter climate too, is severe. "Thirty below weather" and several feet of snow are not unusual for northern Minnesota. The forests in the early days consisted of dense stands of pine, birch, fir, and spruce, but forest fires and lumbering operations have taken away some of the primeval beauty. The animal life is typically northern. Moose, deer, bear, wolves, beaver, muskrat, mink, and porcupines are frequently seen, especially in the part included in the Superior National Forest. The region is the nesting ground of warblers, water fowl, and myriads of other migratory birds, but during the winter the bird population is reduced to woodpeckers, ravens, owls, grosbeaks, siskins, crossbills, and chickadees. Life in such a region is a strenuous undertaking for man. The human population is sparse and only the northern European nationalities and Chippewa Indians are permanent settlers.

About this region and its inhabitants Mrs. Jaques has written a fascinating account of part of one winter's adventure in which she and her husband participated. Through her descriptions, the reader comes to feel the seriousness of everyday life in this back country, but he also feels keenly a charm in its primitive simplicity. Mrs. Jaques has a style of writing that is graphic, lively, and intensely human.

The illustrations, the work of Mr. Jaques, are black and white drawings which contribute much to the vividness of the book. The accuracy and choice of subjects is testimony of his worth as a naturalist and artist. Black and white, with their sharp contrasts, are very effective in portraying a country of deep snow, evergreen foliage, rugged basalt cliffs, and the black and white colors so common to the winter birds and animals.

Though existence in wilderness Minnesota is severe in the eyes of the city person, it has an air of adventure that many would like to sample. The authors have caught this feeling and have presented it effectively. Whether the reader is a winter out-of-doors person or likes to sit before his fireplace and get adventures synthetically, he will find much to enjoy in this little volume.—L. R. WILSON, Coe College, Cedar Rapids, Iowa.

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